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ARTICLE

LATEST CRETACEOUS MULTITUBERCULATES OF THE BLACK BUTTE STATION LOCAL FAUNA (LANCE FORMATION, SOUTHWESTERN WYOMING), WITH IMPLICATIONS FOR COMPOSITIONAL DIFFERENCES AMONG MAMMALIAN LOCAL FAUNAS OF THE WESTERN INTERIOR

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ABSTRACT—Latest Cretaceous (Lancian) mammalian faunas of the Western Interior of North America are mostly known from the northern Great Plains and coastal lowland paleoenvironments. Here, we describe a sample of 143 multituberculate mammal teeth from the Lance Formation of southwestern Wyoming. The specimens, which are from two independent collections made in the 1970s by the University of California Museum of Paleontology and the University of Wyoming Geological Museum, are part of the best-sampled local fauna from the central part of the Western Interior. Deposits of the Lance Formation in this region are on the eastern flank of the Rock Springs Uplift near Black Butte Station. The Black Butte Station local fauna was farther west and possibly paleoenvironmentally distinct from most other Lancian local faunas known. The fossil assemblage preserves eight genera and 11 species of multituberculates. There are many common Lancian taxa, a high relative abundance of *Cimexomys*, the second published occurrences of *Parikimys* and *Paressonodon*, and a new species of *Cimolodon*. Cluster and ordination analyses of multituberculate abundance data from well-sampled Western Interior local faunas show that the Black Butte Station local fauna is distinct from all other local faunas and that variation among mammalian local faunas in composition is correlated with latitude, though paleoenvironmental, temporal, and taphonomic differences may also be factors. Results highlight that explorations in undersampled regions and paleoenvironments are critical to a more complete understanding of the Cretaceous-Paleogene transition.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The Cretaceous-Paleogene (K-Pg) mass extinction event ca. 65.6 million years ago (Ma) marks a critical transition from dinosaur- to mammalian-dominated terrestrial ecosystems. The backdrop to this transition is best documented in the Lancian (ca. 69–65.6 Ma) North American land mammal 'age' (NALMA; Clemens, 2001; Cifelli et al., 2004). Mammalian local faunas of this age are well known throughout the northern Great Plains, from Alberta (e.g., Lillegraven, 1969) to Saskatchewan (e.g., Storer, 1991; Fox, 1997), Montana (e.g., Simpson, 1927; Archibald, 1982; Lofgren, 1995; Clemens, 2002; Wilson, 2005, 2009), North Dakota (e.g., Hunter et al., 1997; Pearson et al., 2002; Hunter and Archibald, 2002), and Wyoming (e.g., Clemens, 1964, 1966, 1973; Webb, 2001). Together, they provide a rich yet somewhat myopic view of mammalian taxonomic diversity and community structure during this interval. In addition to being geographically biased toward northern latitudes (Wilson et al., 2010:fig. 1), the local faunas are almost entirely from deposits that represent coastal lowland paleoenvironments (Fox, 1968), adjacent to the Western Interior Seaway.

This study focuses on the Lance Formation of the eastern flank of the Rock Springs Uplift, near Black Butte Station in southwestern Wyoming (Fig. 1). These deposits are farther south than those that have yielded most Lancian local faunas (Wilson et al., 2010:fig. 1). They also represent an undersampled paleoenvironment, an area inland from the Western Interior Seaway that had positive elevation above sea level during the Late Cretaceous (Mederos et al., 2005). Fossil collecting in the Black Butte Station area dates back to at least 1872 with a party led by F. B. Meek and H. M. Bannister (Breithaupt, 1999). They excavated a large ceratopsid dinosaur from the area that was named *Agathaumas sylvestris* (Cope, 1872); this taxon is now considered nomen dubium and possibly synonymous with *Triceratops* sp. (Breithaupt, 1999). Following this initial field work, fossil collecting in the area was minimal until the 1970s. In 1974, D. Lawson and M. K. Brett-Surman, then from the Department of Paleontology at the University of California, Berkeley, discovered a vertebrate microfossil locality (UCMP locality V-84215), but did not publish the results of their findings. In 1976, vertebrate paleontologists from the University of Wyoming led by J. A. Lillegraven relocated, surface collected, and quarried Lawson's quarry (UW locality V-79032 = UCMP locality V-84215). B. H. Breithaupt, then a graduate student at the University of Wyoming, returned to the area in 1979 to surface collect and screenwash quarried sediment. The University of Wyoming's fossil samples of the Black Butte Station local fauna were then incorporated into Breithaupt's M.S. thesis and the publication that resulted from his thesis (Breithaupt, 1982). Whereas Breithaupt (1982) included detailed descriptions and a community analysis of the non-mammalian vertebrates, mammal fossils were, in most cases, only tentatively identified to genus and not fully described.

The fossil assemblage from the Black Butte Station area comprises two localities (UCMP V-84215 = UW V-79032; UW

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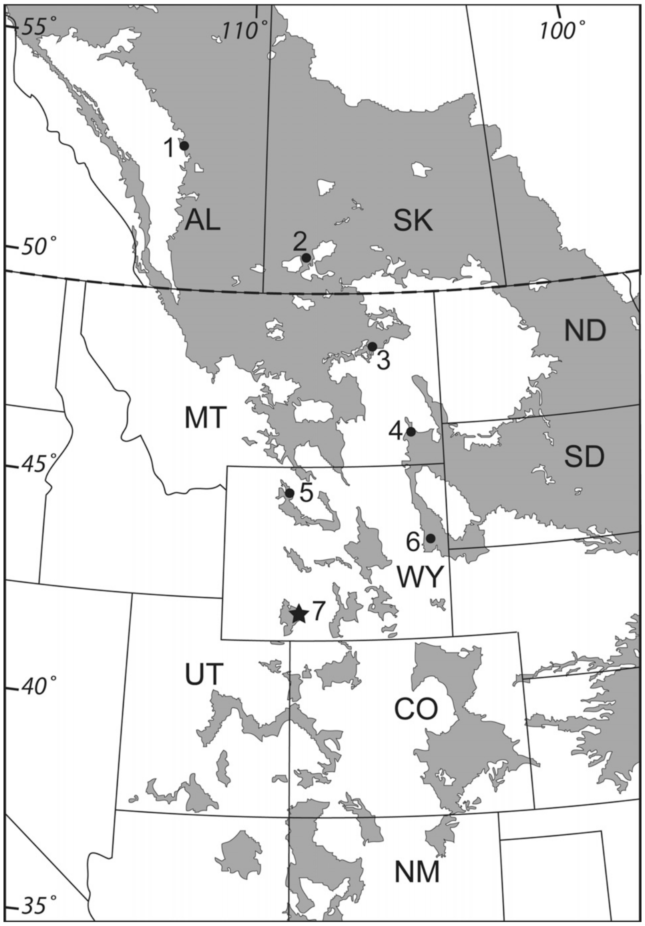

FIGURE 1. Map of the Western Interior of the United States and Canada showing latest Cretaceous well-sampled (n > 90) Lancian mammal localities and Upper Cretaceous sedimentary rocks (modified from Garrity and Soller, 2009, and Wilson et al., 2010). **1**, Trochu local fauna, Scollard Fm., Alberta; **2**, Gryde local fauna, Frenchman Fm., Saskatchewan; **3**, Garfield and McCone counties assorted local faunas, Hell Creek Fm., Montana; **4**, Ekalaka local faunas, Hell Creek Fm., Montana; **5**, Hewitt's Foresight One local fauna, Lance Fm., Wyoming; **6**, Type Lance local fauna, Lance Fm., Wyoming; **7**, Black Butte Station local fauna, Lance Fm., Wyoming (this study).

V-79033) and over 200 mammalian specimens. Here, we describe the 143 specimens that represent the multituberculate component of the Black Butte Station fossil assemblage. The therian component will be described elsewhere. We also detail the geologic setting of the fossil localities and discuss the paleogeographic and paleoecologic implications of these data. Using multituberculate abundance data from the Black Butte Station local fauna and other well-sampled Lancian local faunas from the Western Interior, we use cluster and ordination methods to test for geographic patterns in the community structure data. The results underscore the need for further exploration in undersampled regions and paleoenvironments, to achieve a more complete understanding of the K-Pg transition in North America.

Institutional Abbreviations—**DMNH**, Denver Museum of Nature & Science, Denver, Colorado, U.S.A.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.; **UW**, University of Wyoming Departmental Scientific Collections of the Department of Geology and Geophysics, Laramie, Wyoming, U.S.A; **UWBM**, University of Washington Burke Museum of Natural History and Culture, Seattle, Washington, U.S.A; **YPM**, Yale University Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

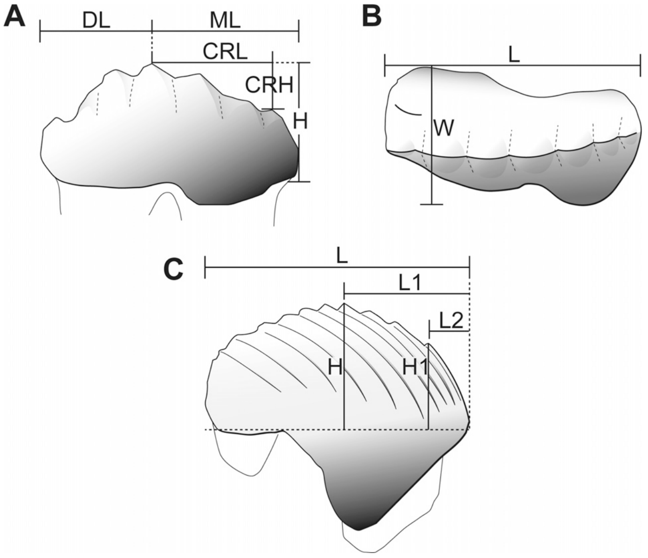

FIGURE 2. Schematic illustration of a multituberculate right P4 in **A**, buccal view and **B**, occlusal view, with measurement standards for length (L), width (W), distal length (DL), mesial length (ML), climbing ratio length (CRL), climbing ratio height (CRH), and height (H). Schematic illustration of a multituberculate right p4 in **C**, buccal view, with measurement standards for length (L), length to highest point in lateral profile (L1), length to first serration (L2), height (H), and height to first serration (H1).

Dental Terminology, Conventions, and Measurements—The dental terminology used follows Simpson (1937) and Jepsen (1940). Cusp formulae for multituberculates are presented from the external row to the internal row (e.g., 7:8:6), an R denotes presence of a non-cuspidate ridge on either M1 or M2 (e.g., 7:8:R). Dental measurements (Fig. 2) follow Clemens (1964), Novacek and Clemens (1977), Hunter et al. (1997), and Eaton (2002). Specimen orientation of isolated P4s/p4s follows Novacek and Clemens (1977) and Eaton (2002). Specimens were measured using a Leica MZ9.5 binocular dissecting microscope and custom measuring stage that has the capability of reading to 0.001 mm.

Measurement Abbreviations—**L**, length; **DL**, distal length; **ML**, mesial length; **W**, width; **DW**, distal width; and **MW**, mesial width. For p4s, **H**, height sensu Novacek and Clemens (1977); **H1**, height 1 sensu Hunter et al. (1997); **L1**, length 1 sensu Novacek and Clemens (1977); and **L2**, length 2 sensu Hunter et al. (1997). **BR**, buccal ridges; **LR**, lingual ridges; and **SE**, serrations. For P4s, **CRH**, climbing ratio height sensu Eaton (2002); and **CRL**, climbing ratio length. '≥' indicates a minimum measurement.

GEOLOGIC SETTING

The Black Butte Station fossil localities are located on the eastern flank of the Rock Springs Uplift in Sweetwater County, Wyoming. The Rock Springs Uplift is a north-south trending antiformal structure that formed in the Late Cretaceous–early Eocene in connection with the Douglas Creek arch to the south (Mederos et al., 2005). Presently, the uplift is exposed as a roughly 96 km by 64 km asymmetric, west-vergent antiformal structure in the middle of the greater Green River Basin, which consists of the Green River subbasin to the west and the Washakie and Sandwash subbasins to the east (Fig. 3). The

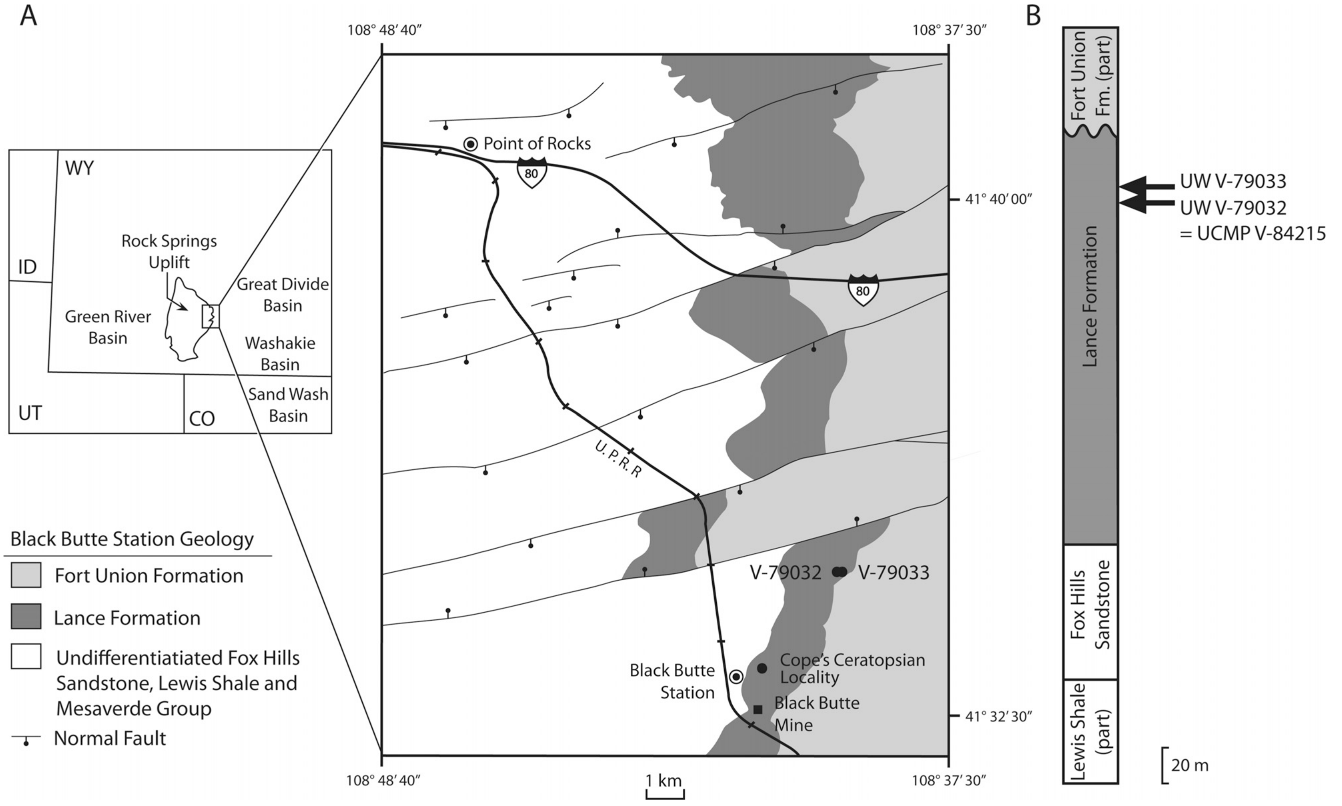

FIGURE 3. **A**, map of Wyoming showing location of Rock Springs Uplift, and generalized geology of the Black Butte Station study area, modified from Breithaupt (1982), Love and Christiansen (1985), and Madden (1989). Google Earth imagery was used to supplement data from Love and Christiansen. U.P.R.R stands for Union Pacific Railroad. **B**, stratigraphy of uppermost Cretaceous and lowermost Paleocene units with position of fossil localities. Locality position is based on field measurements in relation to the base of the Fort Union formation. Unit thicknesses taken from Madden (1989).

Uinta Uplift separates it from the Douglas Creek arch to the south (Mederos et al., 2005). The rock units included in the Rock Springs Uplift are Late Cretaceous–Paleogene in age; the Lance Formation occurs above the underlying Fox Hills Sandstone, and lies below the Paleocene Fort Union Formation (Fig. 3). These units are uncomformably overlain by the Paleocene–Eocene Green River Formation. On the west flank of the uplift, where the rock units dip from 4° to 35° west, the Fox Hills Sandstone, Lance Formation, and Fort Union Formation are notably absent, likely due to erosion (Breithaupt, 1982). On the eastern flank, where the rock units dip from 5° to 8° east (Breithaupt, 1982), these units are present but were deposited unconformably, implying tectonic control of sedimentation (Mederos et al., 2005). The study area may have been significantly above sea level five times during the Late Cretaceous, associated with uplift events during the Laramide Orogeny (Roehler et al., 1977).

In the study area, the Lance Formation is exposed as a 56 km wide by 10 km long, crescent-shaped belt of low-lying sandstone and mudstone hills (Breithaupt, 1982). Thicknesses of the formation range from 85 to 222 m. It is composed primarily of mudstones in various shades of gray, with resistant, lenticular sandstones throughout. The sandstones vary from the thick, basal sands, which tend to have structural bedding and large clast size, to the massive, upper sands. Subbituminous coal seams occur irregularly in the lower portion of the Lance Formation, and in scarce thin lenses in the upper portion (Fig. 3). The seams in the lower half indicate deposition in swampy, brackish lagoons behind barrier sandbars (Roehler et al., 1977). This swampy to marshy floodplain was a densely vegetated, riparian environment. The vertebrate fossil-bearing horizons occur in the upper half of the Lance Formation primarily in the variably colored, somber, dark-gray to brownish-gray mudstones containing carbonaceous detritus (Breithaupt, 1982). Source rocks for deposition of the Lance Formation came from the western tectonically active Mesocordilleran belt. Locally in the Black Butte area, the ancestral Granite Mountains area and Sierra Madre-Medicine Bow complex may have been sources to the east (Breithaupt, 1982). This implies that the Lance Formation from the eastern Rock Springs Uplift, and the type Lance Formation from Niobrara County, Wyoming, were in separate and distinct basins of deposition (Breithaupt, 1982). Deposition of the Lance Formation occurred during the final Mesozoic regression of the Western Interior Seaway off of the North American continent to the east and southeast (Breithaupt, 1982).

The Lance Formation intertongues with the underlying Fox Hills Sandstone. The Fox Hills Sandstone is a cliff-forming unit, which weathers white-gray in contrast to the dark, carbonaceous shales of the lower part of the Lance Formation. As a result, the formational contact between these units is distinct (Breithaupt, 1982). Root zones in the upper part of the Fox Hills Sandstone likely formed from the swamps present during deposition of the lower part of the Lance Formation (Breithaupt, 1982). There is a slight (<10°) angular unconformity between the Lance Formation and overlying Fort Union Formation. The best indicator of the formational contact is a laterally extensive paleosol in the basal Fort Union Formation (Winterfeld, 1982). The paleosol is absent in parts of the study area; in its place is a buff-colored, resistant, medium coarse-grained, conglomeratic channel sandstone deposit. Presumably, the high-velocity streams that deposited these channel sandstones eroded away the paleosol. This basal paleosol–conglomeratic sandstone unit occurs 10.7 m below the first Paleocene coal (Breithaupt, 1982).

DESCRIPTION OF FOSSIL LOCALITIES

Robber's Roost

UW V-79032 (= UCMP V-84215, Lawson Micro). The vast majority (~93%) of mammalian fossils come from this highly fossiliferous locality. The lithology is a gray-brown-colored mudstone with invertebrate fossils and carbonaceous detritus deposited in a paludal stream environment. Abundant leaf impressions are preserved in a resistant, buff sandstone layer overlying this fossil horizon.

Dino Ray

UW V-79033. A smaller percentage of material came from this site, which is 61 m east of, and 10 m higher in section than, UW V-79032. The lithology is a resistant, buff-colored channel sandstone with medium-course and angular to subrounded grains.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
ALLOTHERIA Marsh, 1880
MULTITUBERCULATA Cope, 1884
CIMOLODONTA McKenna, 1975
PTILODONTOIDEA Sloan and Van Valen, 1965
NEOPLAGIAULACIDAE Ameghino, 1890
MESODMA Jepsen, 1940
MESODMA FORMOSA (Marsh, 1889a)
(Fig. 4A, B; Supplementary Data, Table 1S)

Referred Specimens—UCMP 197624, isolated right m1; and UCMP 197636, isolated left m2, both from UCMP locality V-84215 (= UW loc. V-79032). UW 15183, isolated right m1; UW 20077, isolated left m1; UW 15175, 15187, 25162, isolated right m2s; UW 15150, 15168, 15189, 20038, and 20068, isolated left M2s; and UW 15185, isolated right M2, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—m1, m2: All specimens are in full agreement with lower molar descriptions of *M. formosa* in Clemens (1964) and Archibald (1982) and crown dimensions in Webb (2001).

M2: The Black Butte Station specimens match, in most respects, the descriptions and measurements in Lillegraven (1969) and Archibald (1982) for M2s of *M. formosa*. They differ only slightly in cusp formula from the type Lance Formation and Hell Creek Formation samples. Five of six specimens have four internal cusps, whereas one has three internal cusps. Archibald (1982), in contrast, reported that only on rare occasion do specimens from the Hell Creek Formation have four rather than three cusps in the internal row. We nevertheless consider this an acceptable level of intraspecific variation.

MESODMA THOMPSONI Clemens, 1964
(Fig. 4C; Supplementary Data, Table 1S)

Referred Specimens—UCMP 197616 and 197650, isolated left m1s, both from UCMP locality V-84215 (= UW loc. V-79032). UW 15152 and 20153, isolated left m2s; and UW 15164, 20106, isolated right m2s, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—All specimens are in agreement with lower molar descriptions of *M. thompsoni* by Clemens (1964) and Archibald (1982) and crown dimensions in Webb (2001:table 5).

MESODMA cf. *M. THOMPSONI* Clemens, 1964
(Supplementary Data, Table 2S)

Referred Specimen—UW 20145, isolated left p4 from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—UW 20145 was severely damaged postmortem. The mesial third of the crown is absent, and enamel is present on only the dorsal aspect of the crown.

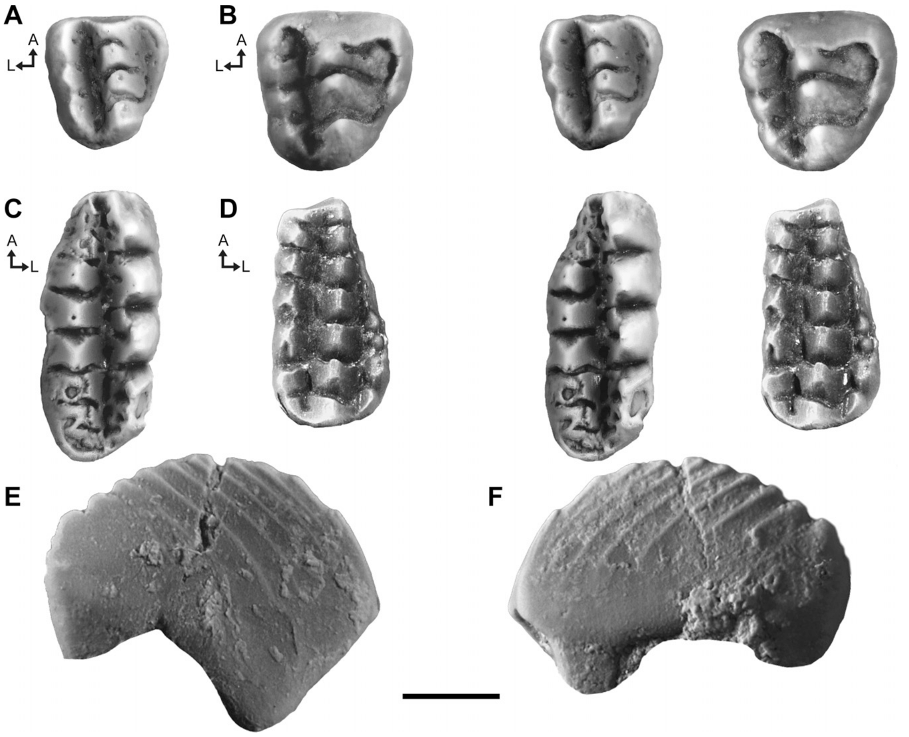

FIGURE 4. *Mesodma formosa*, left M2 (UW 15150) in **A**, stereo occlusal view; left M2 (UW 15189) in **B**, stereo occlusal view. *M. thompsoni*, left m1 (UCMP 197616) in **C**, stereo occlusal view. *M. hensleighi*, right M1 (UW 20118) in **D**, stereo occlusal view. *Parikimys carpenteri*, right p4 (UW 20162) in **E**, buccal view and **F**, lingual view. Arrows indicate anterior (A) and lingual (L) directions. Scale bar equals 1 mm.

Nine serrations are preserved. The morphology of UW 20145 is consistent with descriptions of p4s of *Mesodma* by Clemens (1964). We tentatively assigned it to *M. thompsoni* based on its relatively large size, high serration count, and low distal crown height.

MESODMA HENSLEIGHI Lillegraven, 1969

(Fig. 4D; Supplementary Data, Tables 1S and 2S)

Referred Specimens—UW 15157, isolated left p4; UW 15172, isolated right m1; UW 15190, isolated left m2; and UW 20118 and 20146, isolated right M1s, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—p4: UW 15157 lacks enamel on its lingual and buccal faces and the crown appears to have been crushed postmortem along its mesiodistal axis. Only a few serrations remain intact, but the overall arc profile matches descriptions of *Mesodma* by Clemens (1964). The small size of UW 15157 allows assignment to *M. hensleighi.*

m1: UW 15172 agrees with the description of *M. hensleighi* by Lillegraven (1969).

m2: UW 15190 is poorly preserved, but based on preserved pulp cavities, we estimated a cusp formula of 3:2, which is in agreement with m2s of *Mesodma* (Clemens, 1964). The overall size of the crown falls within the range for *M. hensleighi* given by Archibald (1982).

M1: UW 20118 is moderately worn but the inferred cusp formula (6:7:6) differs slightly from that given by Lillegraven (1969) for M1s of *M. hensleighi* (4–5:8–9:6–7). The medial cusp row is also larger, relative to the external and internal cusp rows, than what is typical for *Mesodma* (Fig. 4D). UW 20146 is somewhat smaller (L = 1.76 mm) than described M1s of *M. hensleighi*, the smallest known Lancian multituberculate (2.10–2.60 mm; Archibald, 1982). We interpret these differences as intraspecific variation.

MESODMA, sp.

(Supplementary Data, Table 1S)

Referred Specimens—UW 15160 and 20076, isolated left m1s; UW 20045, 20079, and 20121, isolated right m1s; and UW 20049, isolated right m2, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—All specimens are consistent with descriptions of lower molars of *Mesodma* (Clemens, 1964). However, because species of *Mesodma* are distinguished from one another based largely on crown dimensions (see Webb, 2001, for discussion) and many of the specimens included here are intermediate in size relative to published measurements, we cannot confidently identify them below the genus level. For example, UW 15160 and 20079 are intermediate in size between m1s of *M. formosa* and *M. thompsoni* (Webb, 2001), whereas UW 20045, 20076, and 20121 are intermediate in size between m1s of *M. hensleighi* and *M. formosa* (Webb, 2001).

PARIKIMYS Wilson, Dechesne, and Anderson, 2010

PARIKIMYS CARPENTERI Wilson, Dechesne, and Anderson, 2010

(Fig. 4E, F; Supplementary Data, Tables 2S and 3S)

Referred Specimens—UW 20052, isolated right p4; UW 20135 and 20137, isolated right m1s; and UW 15191, isolated left m1, all from UW locality V-79032 (= UCMP loc. V84215). UW 20162, isolated right p4, from UW locality V-79033.

Description and Discussion—p4: UW 20162 is well preserved, except for a crack extending vertically from the fourth serration midway down the crown. The crown has a total of 10 serrations. In lateral profile, the crown is moderately tall and arcuate, with the apogee at the fifth serration. The mesial serrations are prominent but rounded as in *Parikimys carpenteri* and *Mesodma thompsoni*, and less robust and angular than those of ?*Neoplagialaux burgessi* and *Cimolodon nitidus*. Distally, the serrations are increasingly rounded as in the distal serrations of *P. carpenteri* and ?*N. burgessi.* The presence of eight buccal and lingual ridges of UW 20162 compares favorably with ridge counts for p4s of *P. carpenteri* and *M. thompsoni* but is less than the number in p4s of *C. nitidus* and ?*N. burgessi*. The first of the buccal ridges follows the mesial edge of the arc profile, whereas the base of the second buccal ridge originates at the base of the first and is mesially convex. The third through eighth buccal ridges are parallel to the second ridge, and distally they become increasingly convex and more widely spaced. A slight dorsobuccal wear cup is present below the ninth and 10th serrations (Fig. 4E). The first lingual ridge follows the mesial aspect of the arc profile, the second through fourth ridges originate independently, are mesially convex, closely spaced, and parallel to each other. The fifth through eighth ridges become increasingly mesially convex and are spaced farther apart towards the distal end of the crown (Fig. 4F). The mesial aspect of UW 20162 slopes dorsodistally, forming a sharp 60° angle with the horizontal (L2:L = 0.17). This profile is similar to p4s of both *P. carpenteri* (L2:L = 0.15 for DMNH 52512) and ?*N. burgessi* (L2:L = 0.22 for UCMP 116896), and differs from those of *M. thompsoni*, which have a nearly vertical mesial aspect (L2:L = 0.07 for *M. thompsoni* UCMP 81650). The mesiobuccal lobe meets the mesial face of the crown at a distinct point as in *P. carpenteri* and ?*N. burgessi*, and forms a mesiobasal concavity that likely accommodated a peg-like p3. The crown is somewhat tall (H:L = 0.45), most similar to *P. carpenteri* (0.46 for DMNH 52512) and the species of *Mesodma* (0.42–0.59; Eaton, 2002:table 1), and ?*N. burgessi* (0.50 for UCMP 116896), but is shorter than *C. nitidus* (0.55–0.64; Eaton, 2002:table 1). Similar to *P. carpenteri*, the distal crown profile becomes decreasingly arcuate, creating an overall profile less symmetric than in ?*N. burgessi* and *C. nitidus* but more symmetric than in *M. thompsoni*. UW 20162 is 10% smaller than the only previously known p4 of *P. carpenteri* (holotype DMNH 52512; see Supplementary Data, Table 2S), but it compares favorably in all other morphological aspects.

UW 20052 suffered postmortem damage, resulting in the loss of the mesial aspect of the crown, the loss of much of the enamel on the ventral portion of the buccal face, the loss of enamel on the dorsal portion of the lingual face, and a chip between the fourth and fifth serrations. Supplementary Data Table 2S lists estimated measurements and serration and ridge counts. The serrations present are rounded and become increasingly robust and bulbous distally. The ridges present both lingually and buccally are as described for UW 20162. In lateral view, the crown is tall (H:L ~ 0.51), arcuate, and nearly symmetric. The distal portion of the arc profile is slightly asymmetric. The mesial aspect of the p4 profile is largely broken on UW 20052, but we tentatively interpret a dorsodistally sloping mesial aspect. On this basis and on the basis of the robust rounded ridges, closely spaced anterior lingual ridges, and an asymmetric distal arc profile, we tentatively assign UW 20052 to *Parikimys carpenteri*.

m1: UW 15191, 20135, and 20137 are well-preserved specimens with little to no wear or postmortem damage. Although distinguishing isolated m1s of similarly sized taxa has historically been difficult (see discussions by Lillegraven, 1969, and Webb, 2001), the specimens from the Black Butte Station local fauna are consistent with the description and diagnosis of *Parikimys carpenteri* (Wilson et al., 2010). In particular, these specimens share the same cusp count, cusp morphology, and waisting at the mid-crown found in the m1 of the holotype (DMNH 52224). As was the case for the p4s, the m1 crown dimensions are smaller than those for the holotype (Supplementary Data, Table 3S). The length of the smallest specimen in our sample (UW 15191, L = 2.09 mm) is 20% smaller than the m1 of DMNH 52224. The length of the smallest newly described p4 of *Parikimys carpenteri* (UW 20052, L = 3.24 mm) is also 20% smaller than the p4 of DMNH 52224. Until sample sizes of *P. carpenteri* from the type area and from Black Butte Station are large enough for statistical

TABLE 1. Frequency of occurrence and percent abundance data of the Black Butte Station local fauna at the species (top) and generic (bottom) levels.

	Tooth position							Percent abundances	
Genus and species	p4	m1	m2	P4	M1	M2	Total	n = 143	n = 106*
Mesodma hensleighi	1	1	1	—	2	—	5	3.50%	4.72%
Mesodma formosa	—	3	4	—	—	6	13	9.09%	12.26%
Mesodma thompsoni	—	2	4	—	—	—	6	4.20%	5.66%
Mesodma cf. *M. thompsoni*	1	—	—	—	—	—	1	0.70%	0.94%
Mesodma, sp. indet.	—	5	1	—	—	—	6	4.20%	5.66%
Parikimys carpenteri	2	3	—	—	—	—	5	3.50%	4.72%
Cimolodon nitidus	1	4	8	5	7	2	27	18.88%	25.47%
Cimolodon cf. *C. nitidus*	2	2	3	—	—	3	10	6.99%	9.43%
Cimolodon peregrinus	1	—	—	—	—	—	1	0.70%	0.94%
Meniscoessus robustus	—	2	1	2	—	—	5	3.50%	4.72%
Meniscoessus cf. *M. robustus*	1	—	—	—	—	—	1	0.70%	0.94%
Essonodon browni	1	2	1	—	1	—	5	3.50%	4.72%
Paressonodon nelsoni	—	—	2	—	1	2	5	3.50%	4.72%
Cimexomys minor	—	—	—	1	7	—	8	5.59%	7.55%
Cimexomys cf. *C. minor*	—	—	—	4	—	2	6	4.20%	5.66%
Cimexomys, sp. indet.	—	—	—	—	1	—	1	0.70%	0.94%
Paracimexomys priscus	—	—	—	—	1	—	1	0.70%	0.94%
?Neoplagiaulacidae	3	7	12	—	—	2	24	16.78%	—
Multituberculata, indet.	3	—	3	—	4	3	13	9.09%	—
Totals							143	100%	100%

	Tooth position							Percent abundances	
Genus	p4	m1	m2	P4	M1	M2	Total	n = 143	n = 106*
Mesodma	2	11	10	—	2	6	31	21.68%	29.25%
Parikimys	2	3	—	—	—	—	5	3.50%	4.72%
Cimolodon	4	6	11	5	7	5	38	26.57%	35.85%
Meniscoessus	1	2	1	2	—	—	6	4.20%	5.66%
Essonodon	1	2	1	—	1	—	5	3.50%	4.72%
Paressonodon	—	—	2	—	1	2	5	3.50%	4.72%
Cimexomys	—	—	—	5	8	2	15	10.49%	14.15%
Paracimexomys	—	—	—	—	1	—	1	0.70%	0.94%
?Neoplagiaulacidae	3	7	12	—	—	2	24	16.78%	—
Multituberculata indet.	3	—	3	—	4	3	13	9.09%	—
Total							143	100%	100%

*Excluding ?Neoplagiaulacidae and Multituberculata indeterminate.

analysis, we conservatively interpret these size differences as intraspecific variation.

CIMOLODONTIDAE McKenna, 1975
CIMOLODON (Marsh, 1889b)
CIMOLODON NITIDUS (Marsh, 1889b)
(Fig. 5B–D; Supplementary Data, Tables 2S and 4S)

Referred Specimens—UCMP 197632, isolated left m1; UCMP 197654, isolated right m2; UCMP 197662, isolated left m2; UCMP 197652 and 197658, isolated left P4s; UCMP 197623 and 197626, isolated left M1s; and UCMP 197627, isolated right M1, all from UCMP locality V-84215 (= UW loc. V-79032). UW 20089 and 20150, isolated left m1s; UW 15156, isolated right m1; UW 15144 and 15153, isolated left m2s; UW 15146, 15147, and 15169, isolated right m2s; UW 17375, isolated right P4; UW 15184 and 20044, isolated left P4s; UW 15155 and 20058, isolated right M1s; UW 20133, isolated left M1; and UW 20062, isolated left M2, all from UW locality V-79032 (= UCMP loc. V-84215). UW 15582, left dentary fragment with p4; UW 20037, isolated right m2; UW

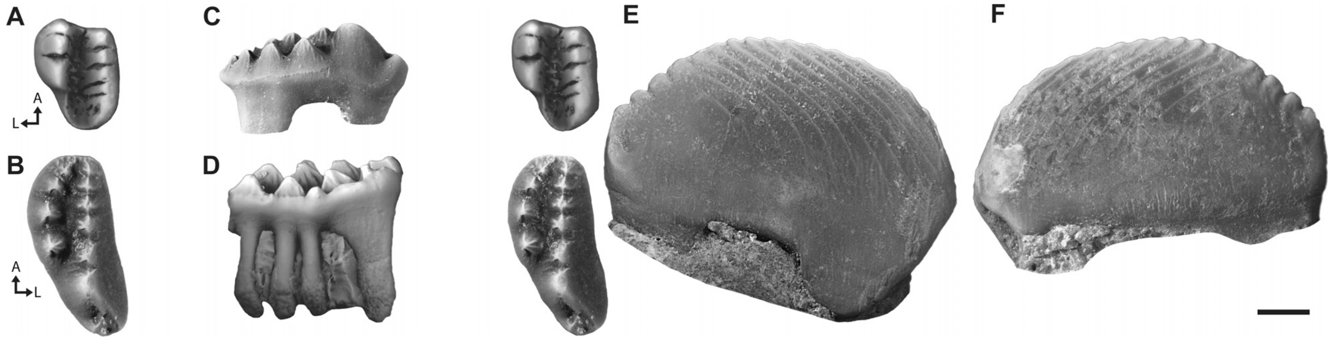

FIGURE 5. *Cimolodon* cf. *C. nitidus*, right m2 (UCMP 197631) in **A**, stereo occlusal view. *Cimolodon nitidus*, right P4 (UW 17375) in **B**, stereo occlusal view and **C**, buccal view; left M1 (UCMP 197623) posterior fragment in **D**, lingual view. *Cimolodon peregrinus*, right p4 (UW 15583) in **E**, buccal view and **F**, lingual view. Arrows indicate anterior (A) and lingual (L) directions. Scale bar equals 1 mm.

15125, isolated left M1; and UW 17376, isolated left M2, all from UW locality V-79033.

Description and Discussion—p4: UW 15582 has a small chip on the apex of the second serration of the crown, but is in good condition otherwise. A small fragment of the dentary spanning the posterior two-thirds of the crown is present, such that the mesial root is exposed. This specimen is moderately worn, with a distobuccal wear cup that spans the three distal-most serrations. The size, morphology, and wear pattern of UW 15582 agree with descriptions of *Cimolodon nitidus* in Clemens (1964).

m1, m2: All specimens compare well in size and morphology with the descriptions of *Cimolodon nitidus* in Clemens (1964) and Archibald (1982). One m2, UW 15144, has an extra internal cusp (cusp formula: 6:3) but is otherwise in agreement with descriptions of m2s of *C. nitidus*. The m2 specimens fall in the lower half of the reported size range of *C. nitidus* m2s (L = 2.3–3.7 mm; Archibald, 1982:table 8). This represents (i) taphonomic bias toward preservation of smaller specimens in the Black Butte Station sample, or (ii) biologically meaningful difference among geographic populations of *C. nitidus*, or (iii) as cautioned by Clemens (1964), the small and large morphs presently assigned to *C. nitidus* represent more than one species.

P4: UW 17375 (Fig. 5B, C) and UCMP 197658 are both well preserved, with slight wear on their lingual faces. UCMP 197658 experienced postmortem damage that removed the enamel along the base of the buccal side of the crown, breaking the bases of the second and third buccal cusps and removing the first entirely. UW 15184, UW 20044, and UCMP 197652 are mesial fragments of P4s, such that each preserves five medial cusps and three or four buccal cusps. Because the morphology of the Black Butte Station specimens is adequately captured by other descriptions of P4s of *Cimolodon nitidus* (Clemens, 1964; Archibald, 1982), we provide no further details.

M1: All specimens compare well with descriptions of M1s of *Cimolodon nitidus* (Clemens, 1964; Archibald, 1982). Because UW 197623 (Fig. 5D) and 197627 are distal fragments and UW 15125 is a mesial fragment, full measurements could not be taken.

M2: UW 20062 and 17367 are both severely worn, such that their cusp morphologies cannot be accurately described. Cusp formula was determined from preserved pulp cavities. Cusp formulae and crown dimensions agree with those in Clemens (1964), though both specimens occur on the low end of the size range (Supplementary Data, Table 4S).

CIMOLODON cf. *C. NITIDUS* (Marsh, 1889b)

(Fig. 5A; Supplementary Data, Tables 2S and 4S)

Referred Specimens—UCMP 197646 and 197651, isolated left p4s; UCMP 197631, isolated right m2, all from UCMP locality V-84215 (= UW loc. V-79032). UW 20170, isolated right m1; UW 25165, isolated left m1; UW 20039 and 20084, isolated right and left m2s, respectively; and UW 20087, 20093, and 20131, isolated right M2s, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—p4: UCMP 197646 and 197651 experienced postmortem damage. In both, only the dorsal half of the crown remains, the enamel is gone from the buccal and lingual faces, and the distal edge of the crown is chipped. Although an exact serration count cannot be made, it is evident that both specimens had a high count. UCMP 197651 is a large fragment that preserves the overall shape of the arc profile fairly well. The ridges are somewhat worn but take a path similar to those of *C. nitidus* (Archibald, 1982; Clemens, 1964). UCMP 197646 is poorly preserved on its mesial edge, such that the overall shape of the arc profile is difficult to determine. The ridge configuration matches descriptions by Archibald (1982) and Clemens (1964). The specimens are referable to *Cimolodon* but are only tentatively referred to *C. nitidus* due to their damaged state and incompleteness.

m1: UW 20170 and 25165 are moderately worn molars. They are consistent with morphological descriptions by Clemens (1964) for m1s of *Cimolodon nitidus*. Their crown dimensions are smaller (UW 20170, L = 3.05 mm; UW 25165, L = 2.94 mm) than those of previously described m1s of *C. nitidus* from the Lance Formation in eastern Wyoming (L = 3.2–4.7 mm; Clemens, 1964) and from the Hell Creek Formation in northeastern Montana (L = 4.48 and 4.53 mm; Archibald, 1982). Clemens (1964) noted a bimodal size distribution among specimens of *C. nitidus* from the Lance Formation and suggested the possibility that the fauna contains two morphologically similar species that are only distinguishable by size. The specimens from the Black Butte Station local fauna would fall among the smaller morph.

m2: All referred specimens match the morphological descriptions for m2s of *Cimolodon nitidus* by Clemens (1964), except for UCMP 197631 (Fig. 5A). The latter has an extra internal cusp (cusp formula: 5:3). Like the m1s described above, the Black Butte Station m2s are somewhat smaller than specimens of *C. nitidus* from the Lance Formation of eastern Wyoming (L = 2.3–3.5 mm; Clemens, 1964).

M2: UW 20087, 20093, and 20131 agree with descriptions of M2s of *Cimolodon nitidus* by Clemens (1964) and Archibald (1982) in all aspects, except overall crown size. All specimens are smaller than described specimens of *C. nitidus* (L = 2.3–3.4 mm; Clemens, 1964), but have similar L:W ratios: 1.17 for UW 20087; 1.13 for UW 20093; 1.11 for UW 20131; and 1.14 for Lance Formation specimens from eastern Wyoming (Clemens, 1964).

In sum, we tentatively refer the above specimens to *C. nitidus*, recognizing that statistical analysis of large samples referred to *C. nitidus* may identify a new smaller species of *Cimolodon*.

CIMOLODON PEREGRINUS, sp. nov.

(Fig. 5E, F; Supplementary Data, Table 2S)

Etymology—From Latin ‘peregrinus’ meaning traveler or wanderer in reference to its discovery in an area distant and inland from most Lancian localities along the coast of the Western Interior Seaway.

Holotype—UW 15583, right dentary fragment with p4.

Type Locality—Dino Ray (UW loc. V-79033) is within a resistant, medium-coarse-grained, subangular to subrounded channel sandstone horizon. It occurs on the eastern flank of the Rock Springs Uplift in Sweetwater County, Wyoming.

Diagnosis—Differing from *Mesodma thompsoni* in: larger p4 with greater number of serrations (16), arcuate mesial face (larger L2:L ratio). Differing from *Cimolodon nitidus* and *Anconodon gidleyi* in: large p4 (L = 7.00 mm) with greater number of serrations, gently sloping, rounded mesial face (smaller L2:L ratio), lower crown (smaller H:L ratio), and a smaller mesiobuccal lobe. Differing from *C. similis* and *C. foxi* in: larger p4 with greater number of serrations, lower crown (smaller H:L ratio). Differing from *Meniscoessus robustus* and *M. seminoensis* in: p4 with rounded, muted serrations, greater number of serrations, arcuate mesial face (larger L2:L ratio), lack of a notched first serration, and overall less robust crown.

Description and Discussion—UW 15583 is a small fragment of a right dentary containing a well-preserved p4. The preserved dentary is as long as the base of the p4 crown and just deep enough to conceal the root apices of the p4. In lateral profile, the p4 arc is symmetrical with the apogee over the fifth serration. The serration count (16) is greater than for any other Lancian multituberculate; *Meniscoessus robustus* has at most 10 serrations (Wilson et al., 2010), *Cimolodon nitidus* has 12 to 14 (Clemens, 1964), and the smaller *Mesodma thompsoni* has 11 to 14 (Archibald, 1982). The serrations are muted at the mesial end of the p4 arc but become increasingly rounded and robust distally, with the final three serrations appearing bulbous. These subdued rounded serrations are most similar to those of *C. nitidus* and differ from the angular robust serrations of *M. robustus.* There are 13 buccal and 13 lingual ridges present (Supplementary Data, Table 2S); all are subtle and indistinct.

The first buccal ridge follows the mesial aspect of the crown (Fig. 5E). The second and third ridges are parallel, intersect the base of the first, and are slightly mesially convex. The anterior ridges are closely spaced mesially and become increasingly convex and more broadly spaced distally. Although the crown lacks a distinct buccodistal wear facet, even slight wear would obliterate a ridge; thus, the presence of additional distal ridges prior to wear cannot be ruled out. The lingual ridges are more closely spaced than the buccal ridges and become increasingly convex distally (Fig. 5F). The mesiobuccal lobe is very small and meets the mesial face of the crown at an obtuse angle, leaving a mesiobasal concavity that presumably housed a peg-like p3. The mesial face is rounded and gently sloping (L2:L = 0.14), differing from (i) the steeply sloping face of *C. nitidus* (0.20 for UCMP 52062); (ii) from the mesial face of *M. robustus* (0.09 for UCMP 46875), which is interrupted by a distinct horizontal notch at the first serration; and (iii) the nearly vertical face of *Mesodma* (0.07 for *M. thompsoni*, UMMP 81650). The first serration of UW 15583 is tall (H1:H = 0.81), comparing most favorably with those of *C. nitidus* (0.81 for UCMP 52062) and *M. robustus* (0.71 for UCMP 46875); it is considerably taller than that of *M. thompsoni* (0.63 for UMMP 81650). The overall height of the crown is tall (H:L = 0.54), only slightly shorter than in *C. nitidus* (0.55–0.64; Clemens, 1964) and *M. robustus* (0.59 for UCMP 46875) but taller than in *M. thompsoni* (0.43–0.53; Eaton, 2002). The overall size of the crown is large (L = 7.00 mm), which is at the high end of the size ranges for both *C. nitidus* and *M. robustus* (L = 5.0–7.1 mm for *C. nitidus* and 5.7–7.1 mm for *M. robustus*; Clemens, 1964). Among Lancian multituberculates, UW 15583 compares most favorably with *C. nitidus*, but the larger number of serrations, rounded mesial face, shorter crown, and smaller mesiobuccal lobe distinguish it as a new species. The presence of a large p4 with a tall arc and a high number of serrations is common to Cimolodontidae (Kielan-Jaworowska and Hurum, 2001). The presence of these characters in UW 15583 allows us to place this new species within *Cimolodon*.

CIMOLODMYIDAE Marsh, 1889b
MENISCOESSUS Cope, 1882
MENISCOESSUS ROBUSTUS (Marsh, 1889a) Osborn, 1891
(Fig. 6A, B; Supplementary Data, Tables 2S and 5S)

Referred Specimens—UCMP 197615, isolated left m1; and UCMP 197655, isolated left P4, both from UCMP locality V-84215. UW 15123, fragmentary right m1; UW 20046, fragmentary right m2; and UW 15195, isolated right P4, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—m1: UW 197615 is well preserved except for a dorsoventral crack that extends between the third and fourth buccal cusps (Fig. 6A, B). Wear is present on the mesial edge of the crown from contact with the adjacent p4. The size and morphology of UW 197615 (see Supplementary Data, Table 5S) fits previously published measurements of m1s of *M. robustus* (Clemens, 1964; Archibald, 1982; Webb, 2001; Wilson,

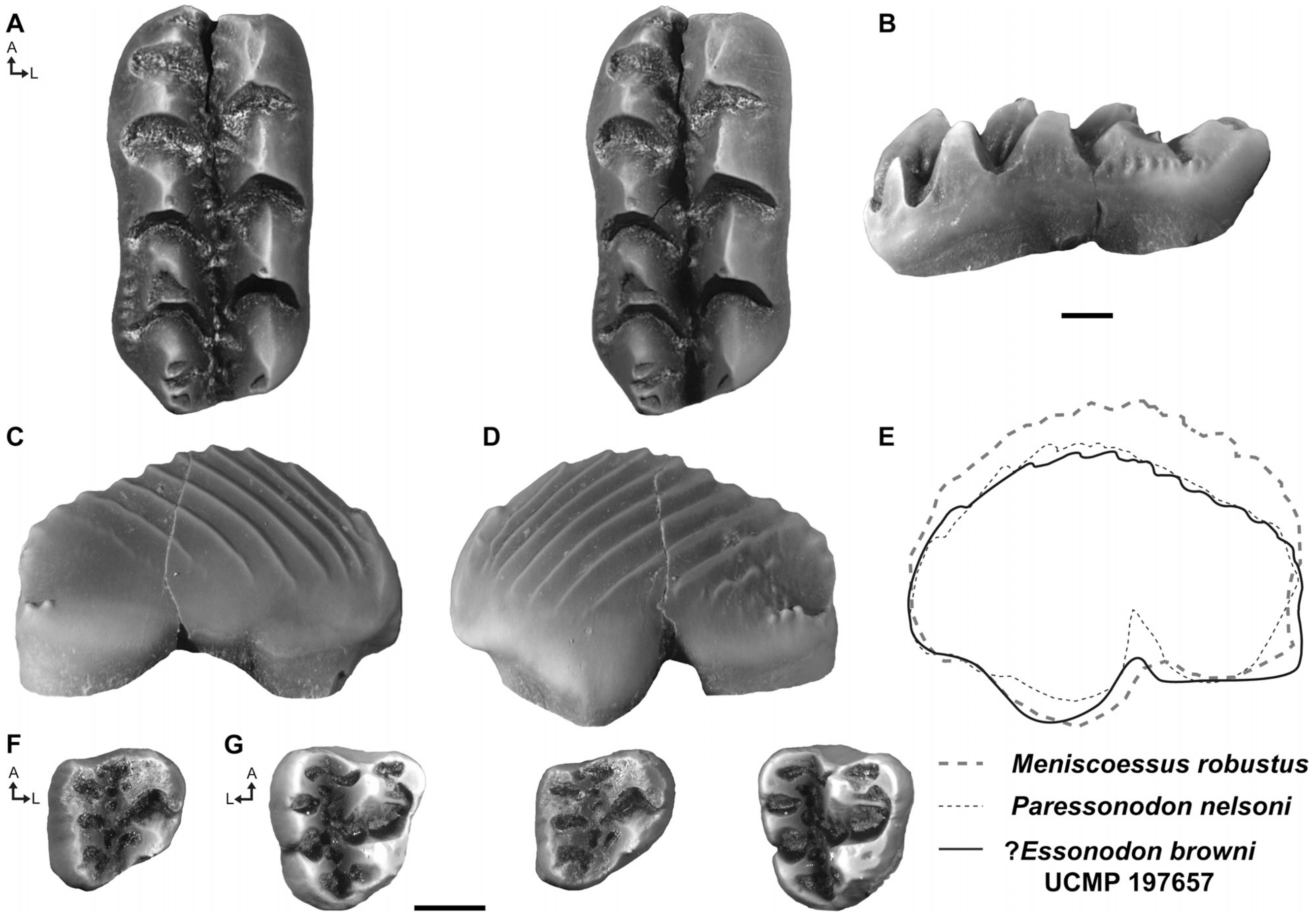

FIGURE 6. *Meniscoessus robustus*, left m1 (UCMP 197615) in **A**, stereo occlusal view and **B**, buccal view. ?*Essonodon browni*, left p4 (UCMP 197657) in **C**, lingual view and **D**, buccal view. **E**, superimposed buccal outlines of p4s. ?*E. browni* (UCMP 197657), black line; *Paressonodon nelsoni* (UWBM 90886), thin dashed line; *Meniscoessus robustus* (UCMP 107405), thick dashed line. *Paressonodon nelsoni*, left m2 (UW 20134) in **F**, stereo occlusal view; left M2 (UW 20041) in **G**, stereo occlusal view. Arrows indicate anterior (A) and lingual (L) directions. Scale bars equal 1 mm.

2004) but is larger, and does not taper mesially as in *M. seminoensis* (Eberle and Lillegraven, 1998a). UW 15123 is a mesiobuccal fragment of m1 with two broken cusps. Each cusp is broken on its occlusal surface and enamel is only preserved around the bases of each. Nevertheless, it is clear that the large cusps were crescentic, as in *M. robustus* (Clemens, 1964).

m2: UW 20046 is a fragment of a large molar crown containing two crescentic, mesiobuccal cusps. The large size and cusp morphology allow us to confidently identify this fragment as an m2 of *Meniscoessus robustus* (Clemens, 1964).

P4: UW 15195 is extremely worn and lacks enamel. There are four medial cusps, which are short, rounded, and indistinct due to wear. There are two mesiobuccal cusps, which are also rounded, and three small cuspules on the distal edge of the tooth. UCMP 197655 lacks the mesial margin of the crown, preserving only the distal edge of the first medial cusp. The enamel on its buccal face is lost, along with any buccal cusps that may have been present. Of the four medial cusps, the second is intact and has a sharp and conical morphology. The distobuccal cusp and the distomedial cusp are both large and connected by a low ridge that follows the distal edge of the crown. Despite heavy wear and postmortem damage, these teeth match published measurements and descriptions of *Meniscoessus robustus* by Clemens (1964) and Archibald (1982).

MENISCOESSUS cf. *M. ROBUSTUS* Marsh, 1889b
(Supplementary Data, Table 2S)

Referred Specimen—UW 20157, right p4 from UW locality V-79033.

Description and Discussion—UW 20157 was broken postmortem such that the buccal face of the tooth is absent and the arc profile is not intact. Nine serrations are present, though more may have been present prior to damage. There does not appear to be an anterior notch, as in *Meniscoessus seminoensis*. The buccal ridges are worn, so an exact ridge count cannot be made. The ridges that are present agree with descriptions of ridge patterning in *M. robustus* given by Archibald (1982). A small distobuccal cuspule is present on UW 20157, a character common to cimolomyids, especially *Meniscoessus.* We tentatively assign UW 20157 to *Meniscoessus* cf. *M. robustus*, but recognize that without a complete arc profile, differentiation between *Essonodon browni*, *M. robustus*, and *M. seminoensis* is difficult (see below).

?CIMOLOMYIDAE Marsh, 1889b

Comments—*Essonodon* and the recently described *Paressonodon* (Wilson et al., 2010) have morphologies that are divergent relative to other members of the Cimolomyidae. They share low molar cusps in cusp rows that are connected by a transverse latticework of variable development. The m2 length-to-width ratios of *E. browni* (L:W = 0.68–0.95; Archibald, 1982) and *P. nelsoni* (L:W = 0.93 for UWBM 92321; Simon and Wilson, unpubl. data) are low and likely derived relative to those found in other cimolomyids (1.4 for *Cimolomys gracilis*, UCMP 110622; 1.6 for *Meniscoessus robustus*, UCMP 116962; Archibald, 1982). The ratio of p4 to m2 lengths (p4:m2) of these taxa might also differ from other cimolomyids. Based on a p4 possibly referable to *E. browni* (see below, UCMP 197657) and an m2 of *E. browni* (UW 25151), the p4:m2 ratio for ?*E. browni* is 3.2. For *P. nelsoni*, the p4:m2 ratio is 2.7 (Simon and Wilson, unpubl. data), again intermediate between ?*E. browni* and other Lancian cimolomyids (1.33 for *Cimolomys gracilis* and 1.57 for *Meniscoessus robustus*; Clemens, 1964). This intermediate position agrees with other morphological features that indicate that *P. nelsoni* is less derived than *E. browni* (Wilson et al., 2010; Simon and Wilson, unpubl. data). Thus, within Cimolomyidae, *Paressonodon* and *Essonodon* share a number of derived features that may eventually necessitate placement of these taxa in their own family. However, until this phylogenetic hypothesis is explicitly tested, we provisionally accept the tentative placement of *E. browni* and *P. nelsoni* in Cimolomyidae (Archibald, 1982; Kielan-Jaworowska and Hurum, 2001).

ESSONODON Simpson, 1927
ESSONODON BROWNI Simpson, 1927
(Supplementary Data, Table 5S)

Referred Specimens—UW 15122, left dentary fragment containing m1; UW 17374, isolated right m1 fragment; UW 25151, isolated right m2; UW 20073, isolated left M2, all from UW locality V-79032 (= UW loc. V-79032).

Description and Discussion—m1: UW 15122 is a left dentary fragment with an m1. The dentary fragment spans only the mesial two-thirds of the m1 crown. The mesial and distal roots are visible and intact. In both buccal and lingual views, the most dorsal portions of accessory roots can be seen, but because they are embedded in the dentary fragment an exact count is not possible. The crown is well preserved, though the cusps are slightly worn. The cusp formula is 7:5. UW 17374 is the mesiobuccal portion of a right m1 with three preserved cusps. The cusp morphology, including the robust internal ridges, is comparable to UW 15122. Both specimens match description of m1s of *E. browni* (Archibald, 1982).

m2: UW 25151 is an isolated right m2 with a cusp formula of 3:2. The crown is moderately worn with dentine exposed on the tips of cusps as well as on the latticework of ridges. The morphology matches the description of Clemens (1964). The L:W ratio for UW 25151 is 0.92, on the larger end of the range for m2s of this species (0.68–0.95; Archibald, 1982).

M2: UW 20073 is well preserved and only differs from the description of M2s of *E. browni* (Archibald, 1982) in having small cuspules on its buccal ridge. It is also slightly smaller (L = 2.39 mm) than the smallest M2 described by Archibald (1982; L = 2.49 mm for YPM 14907), but within what we consider intraspecific variation.

?*ESSONODON BROWNI* Simpson, 1927
(Fig. 6C, D; Supplementary Data, Table 2S)

Referred Specimen—UCMP 197657, left p4, from UCMP locality V-84215 (= UW loc. V-79032).

Comments—The p4, the most diagnostic tooth among multituberculates, is presently unknown for *Essonodon browni*, contributing to the uncertainty in its phylogenetic placement (Simmons, 1993; McKenna and Bell, 1997; Weil, 1999; Kielan-Jaworowska and Hurum, 2001).

Recent description of *Paressonodon nelsoni* (Wilson et al., 2010), a taxon with molar morphology intermediate between *E. browni* and other cimolomyids (see above), provides an opportunity to estimate the p4 morphology of *Essonodon*. The holotype of *P. nelsoni* (UWBM 89450) is a right maxillary fragment with M1–M2. Molar features of this new taxon are slightly more primitive relative to those of *E. browni*. On this basis, *P. nelsoni* was proposed as sister taxon to *E. browni* and tentatively placed within Cimolomyidae (Wilson et al., 2010). UWBM 90886 and UWBM 92321 are two unpublished specimens from the type locality that have been referred to *P. nelsoni* (Simon and Wilson, unpubl. data). UWBM 90886 is a dentary fragment with a p4 and mesial portion of m1. UWBM 92321 is an isolated m2. Referral of these specimens to *P. nelsoni* is justified on the basis of dimensions and the presence of the modest latticework of ridges between molar cusps that is found in the holotype (Simon and Wilson, unpubl. data). The p4 of *P. nelsoni* likely approximates the p4 morphology of its sister taxon, *Essonodon*, and is thus used in comparisons below.

Description and Discussion—UCMP 197657 is a large, well-preserved p4, except for a repaired dorsoventral crack extending from the fifth serration to the base of the crown (Fig. 6C, D). In lateral view, the profile forms a low asymmetrical arc

(H:L = 0.47) that is similar to *P. nelsoni* (0.53 for UWBM 98066) and shorter than *Meniscoessus robustus* (0.59 for UCMP 46875), *Cimolomys gracilis* (0.51 estimated for UCMP 48004; Clemens, 1964), and *Cimolodon* (0.55–0.64 for *Cimolodon nitidus*; Clemens, 1964) (Fig. 6E). The serration count (11) is comparable to that in p4s of *C. nitidus* (12–14; Clemens, 1964; Archibald, 1982) but high relative to p4s of cimolomyids *Meniscoessus robustus*, *M. seminoensis*, *Cimolomys gracilis* (8–10; Clemens, 1964; Lillegraven, 1987; Eberle and Lillegraven, 1998a), and *Paressonodon nelsoni* (9; Simon and Wilson, unpub. data). The mesial aspect of the p4 arc profile is vertical to slightly convex (L2:L = 0.13). The first serration forms a distinct notch. This notch occurs higher on the arc than in both *M. robustus* (L2:L = 0.09 for UCMP 46875) and *P. nelsoni* (L2:L = 0.08 for UWBM 98066) and does not define the apex of a distinct anterior lobe as in *M. seminoensis* (Eberle and Lillegraven, 1998a). The profile rises steeply to the apogee, which occurs mesially at the third serration (L1:L = 0.45). This is intermediate in position relative to p4s of *P. nelsoni* (L1:L = 0.54 for DMNH 52225) and *M. robustus* (L1:L = 0.36 for UCMP 46875). Similar to the p4 of *P. nelsoni*, the arc profile slopes distoventrally at a shallow angle from the fourth to 12th serrations (Fig. 6E). Among the 10 buccal ridges, the first follows the mesial aspect of the crown in a sinuous but overall mesially convex fashion. The second and third ridges originate in close proximity to each other with ventral sinuous irregularities. Distally, the remaining ridges become parallel and mesially convex. The fourth through eighth ridges are robust and parallel to the distal portions of the second and third ridges. The ninth ridge originates at the point of contact between the mesiobuccal and distobuccal lobes and is parallel to the mesial ridges, but in a sinuous fashion. The 10th buccal ridge is sinuous and is worn at its distal end. The configuration of the lingual ridges is similar to the buccal ridges: the first ridge following the mesial aspect of the crown; the ninth and 10th ridges are mesially convex and parallel with sinuous irregularities in many ridges. Distinct cups are present on distal ends of both the buccal and lingual faces of the crown, with accessory cuspules on the mesial rim of each cup. The presence of distal accessory cuspules is common among p4s of *M. robustus* and *C. gracilis* (Clemens, 1964; Wilson et al., 2010), and are also found in *P. nelsoni* (Simon and Wilson, unpub. data). The height of the first serration (H1:H) in UCMP 197657 is 0.73, which is larger than the cimolomyids *P. nelsoni* (0.58 for DMNH 52225) and *M. robustus* (0.71 for UCMP 46875). The dimensions of UCMP 197657 are larger than p4s of other known Lancian multituberculates (L = 5.0–7.1 mm for *C. nitidus* and 5.7–7.1 mm for *M. robustus*; Clemens, 1964). The distal aspect of the p4 is worn, presumably from contact with the mesial aspect of the adjacent m1. Without associated specimens, we cannot confidently say that this large premolar belongs to *Essonodon browni*, and we acknowledge the possibility that this specimen may belong to a new species of *Meniscoessus* or some other large cimolomyid. Because of similarities with the p4 of *P. nelsoni*, and its large dimensions relative to other cimolomyids, we tentatively assign UCMP 197657 to ?*E. browni* until additional specimens are discovered.

PARESSONODON Wilson, Dechesne, and Anderson, 2010
PARESSONODON NELSONI Wilson, Dechesne, and Anderson, 2010
(Fig. 6F, G; Supplementary Data, Table 7S)

Referred Specimens—UCMP 197660, isolated right M2, from UCMP locality V-84215 (= UW loc. V-79032). UW 15167, isolated right m2; UW 20134, isolated left m2; and UW 20041, isolated left M2, all from UW locality V-79032 (= UCMP loc. V-84215). UW 17377, isolated right M1, from UW locality V-79033.

Description and Discussion—m2: UW 20134 and 15167 compare well with UWBM 92321, which Simon and Wilson (unpub. data) have identified as an m2 of *Paressonodon nelsoni* (Fig. 6F). UW 20134 is 14% larger than UWBM 92321 (Supplementary Data, Table 7S). UW 15167 has a L:W ratio of 1.15, which is greater than observed in other m2s referred to *P. nelsoni* (L:W = 1.00 for UWBM 92321 and UW 20134).

M1: UW 17337 is a poorly preserved large M1. The enamel is no longer present, and the cusps have been completely worn away such that the tooth surface is smooth and an accurate cusp count cannot be made. The overall shape of the crown exhibits ‘torsion’ along its mesiodistal axis, suggesting that the molar cusp rows formed a ‘stair-step’ arrangement. This feature is found in M1s of both *Paressonodon nelsoni* (Wilson et al., 2010) and *Essonodon browni* (Archibald, 1982). The overall size of the molar (L = 5.40 mm) is about 10% larger than the M1 of the corresponding tooth on the holotype (L = 4.86 mm for UWBM 89450; Wilson et al., 2010), but much smaller than M1 measurements of *E. browni* (L = 7.45 mm for UCMP 120397; Archibald, 1982). We assign UW 17337 to *P. nelsoni*.

M2: UW 20041 (Fig. 6G) and UCMP 197663 are well-preserved specimens with moderate wear. They are morphologically similar to the M2 of *P. nelsoni* (Wilson et al., 2010), in that they have crescentic cusps interconnected by a robust latticework of ridges. As in the holotype, in lingual or buccal view, the ridgelines form a series of U-shaped undulations. The specimens from Black Butte Station are approximately 10% larger than the holotype (Supplementary Data, Table 9S), and UCMP 197663 has a slightly higher length-to-width ratio (L:W = 1.10) than the holotype M2 (1.00 for UWBM 89450; Wilson et al., 2010). Until more specimens of *P. nelsoni* are known, we attribute these slight size differences to intraspecific variation.

INCERTAE SEDIS
PARACIMEXOMYS Archibald, 1982
PARACIMEXOMYS cf. *P. PRISCUS*
(Fig. 7A; Supplementary Data, Table 8S)

Referred Specimen—UW 20047, isolated right M1 from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—M1: UW 20047 exhibits moderate wear. Its crown dimensions are large (L = 2.76 mm) relative to other taxa in the *Paracimexomys* group (L = 2.2–2.6 mm for *Paracimexomys priscus*; Eaton 2002). In occlusal view, the crown does not exhibit waisting or development of an internal cusp row. The cusp formula is 4:5. The mesial-most two cusps and the large distal cusp in the medial cusp row are broken, which makes the path of this row difficult to follow, and thus the mesial divergence of the two cusp rows is difficult to assess. Here, we consider the cusp rows to diverge slightly. The external cusps are conical to pyramidal. The first external cusp is small and connected by a ridge to the second external cusp. Valleys separate the second, third, and fourth external cusps. The tip of the third external cusp is worn. The fourth external cusp, which is also worn, appears to have been connected to the fifth medial cusp by a ridge that is now obscured by wear. The first and second medial cusps are conical and very worn, but were likely low in height. The third medial cusp is also low and conical, but only slightly worn. The low height of the third medial and external cusps makes UW 20047 appear concave in lateral view. The fourth medial cusp is much larger than more mesial cusps and is moderately worn such that it matches the third medial cusp in height. Despite the wear on the fourth medial cusp, it is evident that its cusp apex was deflected mesially. The fifth cusp is also very large with a mesially deflected apex; it is set more buccally than other cusps in the medial row. Two large ridges extend from its internal and external sides to form a nearly complete ridge along the distal edge of the crown. A low ridge also follows the mesial edge of the crown, connecting both cusp rows. The distal cusps of both rows have one or more vertical ribs on their medial faces that do not extend into the medial valley. Vertical ribs on molars of other members of the *Paracimexomys* group, such as *Dakotamys* (Eaton and

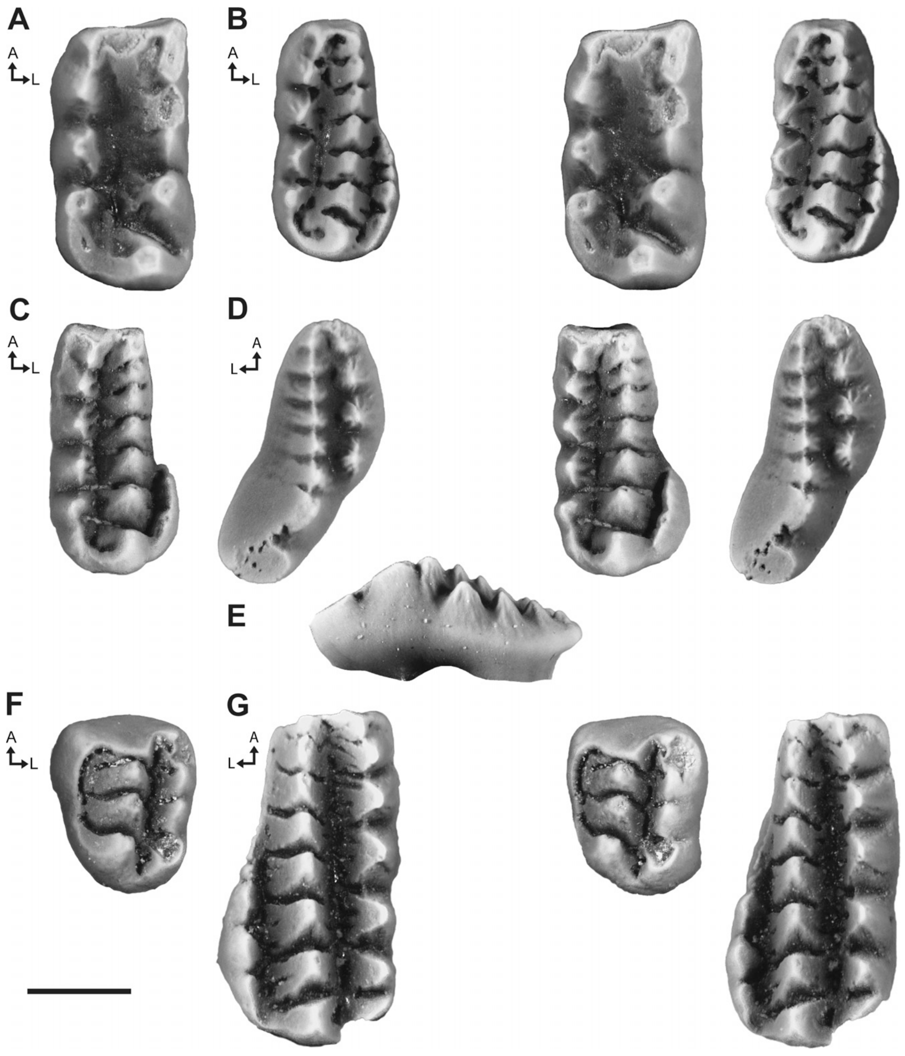

FIGURE 7. *Paracimexomys* cf. *P. priscus*, right M1 (UW 20047) in **A**, stereo occlusal view. *Cimexomys minor*, right M1 (UCMP 197664) in **B**, stereo occlusal view; right M1 (UW 20151) in **C**, stereo occlusal view. *Cimexomys* cf. *C. minor*, left P4 (UCMP 197648) in **D**, stereo occlusal view and **E**, buccal view; right M2 (UCMP 197614) in **F**, stereo occlusal view. *Cimexomys*, sp. indet., left M1 (UCMP 197622) in **G**, stereo occlusal view. Arrows indicate anterior (A) and lingual (L) directions. Scale bar equals 1 mm.

Cifelli, 2001), are more prominent. The base of the medial valley in UW 20047 is smooth, and lacks pits, unlike in *Cedaromys* and *Bryceomys* (Eaton and Cifelli, 2001).

UW 20047 compares most favorably with two genera in the *Paracimexomys* group: the Judithian *Cedaromys* and Judithian–Lancian *Paracimexomys* (Eaton and Cifelli, 2001:table 3). UW 20047, like *Cedaromys*, lacks an internal cusp row, and is relatively large in overall size (L = 2.52–2.64 mm for *Cedaromys bestia*; Eaton and Cifelli, 2001). However, *Cedaromys* also typically has pits and ribbing in its medial valley and a cusp count (4:3) that is lower than in UW 20047. Compared with *Paracimexomys*, UW 20047 has less pitting and ribbing, but compares well in size (L = 2.21–2.60 for *Paracimexomys priscus*; Eaton 2002) and cusp formula for medial and external rows (4–5:4–5:1–2; Eaton and Cifelli, 2001:476). UW 20047 differs from *P. priscus* in that it does not have an internal cusp row, and its occlusal outline does not exhibit waisting (Eaton, 2002). Hunter et al. (2010) recently erected a new species, *Paracimexomys propriscus*, into which they placed newly described specimens from the 'Edmontonian'-aged St. Mary River Formation of northern Montana and transferred Judithian specimens previously assigned to *P. priscus* (Lillegraven and McKenna, 1986; Montellano, 1992). *P. propriscus* is considered to be ancestral to *P. priscus* by Hunter et al. (2010). M1s of *P. propriscus* are morphologically closer to UW 20047 than M1s of *P. priscus* in that they exhibit weak waisting and possess only a single, small internal cusp. However, they differ in that they are smaller in size than UW 20047 (L = 2.11–2.40 mm; Hunter et al., 2010:table 1), and have fewer cusps in the medial row (4:4:1; Hunter et al., 2010). The lack of an internal ridge in UW 20047 is the only character that conflicts with referral of this specimen to *Paracimexomys*. The lack of an internal cusp row in UW 20047 might be intraspecific variation within *P. priscus* or *P. propriscus*, or it could alternatively represent a primitive feature of a new species of *Paracimexomys* that may be ancestral to both of these species. However, based on the large size, high cusp formula for external and medial cusps, and the lack of a waist in UW 20047, we assign this specimen to *Paracimexomys* cf. *P. priscus* but recognize that additional specimens may clarify the relationship of species within *Paracimexomys* and call for reassignment.

CIMEXOMYS Sloan and Van Valen, 1965
CIMEXOMYS MINOR Sloan and Van Valen, 1965
(Fig. 7B, C; Supplementary Data, Tables 2S and 8S)

Referred Specimens—UCMP 197664, isolated right M1, from UCMP locality V-84215 (= UW loc. V-79032). UW 25147, isolated right P4; UW 15188, isolated left M1; and UW 20078, 20088, 20095, and 20151, isolated right M1s, all from UW locality

V-79032 (= UCMP loc. V-84215). UW 17979, isolated right M1, from UW locality V-79033.

Description and Discussion—P4: UW 25147 is unworn, but the tips of the distomedial cusp and the two lingual cuspules are broken. The mesial tooth margin is also broken just above the base of the mesial-most cusps. This specimen matches the description for *C. minor* by Archibald (1982) but is smaller (L = 1.82 mm; Supplementary Data, Table 3S) than previously described specimens (L = 2.30–2.32 mm, Archibald, 1982; L = 2.09–2.25, Lofgren, 1995). Without larger samples for statistical analysis, we take the conservative approach and attribute this size difference to intraspecific variation.

M1: All specimens agree with descriptions and measurements of *Cimexomys minor* by Archibald (1982) and Webb (2001). Notably, there is a bimodality between specimens with a moderately developed buccal shelf that lacks distinct cusps (UW 15188, 20078, 20151), and specimens with three developed buccal cusps (UCMP 197664, UW 17979, 20088, 20095). This may suggest the presence of an additional species of *Cimexomys* or closely related genus.

CIMEXOMYS cf. *C. MINOR* Sloan and Van Valen, 1965
(Fig. 7D–F; Supplementary Data, Tables 2S and 8S)

Referred Specimens—UCMP 197648, isolated left P4; UCMP 197614, isolated right M2, both from UCMP locality V-84215 (= UW loc. V-79032). UW 15192 and 20083, isolated right P4s; UW 20143 isolated left P4; and UW 20097, isolated left M2, all from UW locality V-79032 (= UCMP loc. V-84215).

Description and Discussion—P4: 15192 exhibits extreme wear; both medial and buccal cusp rows are mostly worn away, leaving only slight raised surfaces where the cusps were. The estimated cusp formula is 3:6:? (Supplementary Data, Table 2S), though we acknowledge the possibility of an additional mesial cusp in the medial row. The mesial portion of the tooth experienced intense wear, such that the current height difference between the mesial and distal cusps in the medial row is likely exaggerated. Wear and postmortem damage removed enamel from all but the distobuccal face of the crown. The other P4 specimens have only slight wear and damage. The Black Butte Station P4s range in size with L = 2.30–2.66 mm (Supplementary Data, Table 2S), slightly larger than *Cimexomys minor* (2.09–2.25 mm; Lofgren, 1995:table 19) and smaller than the Puercan *C. gratus* (3.05–3.44; Archibald, 1982:table 16). The cusp formulae are 3:6 (UW 15192, 20143), 4:6 (UW 20083), and 4:7 (UCMP 197648), which are larger than both *C. judithae* and *C. minor* (3:5 for both; Archibald 1982; Montellano et al., 2000) and *C. gratus* (3–4:5–6; Archibald, 1982). The cusp and crown morphology for these specimens is very similar to that for P4s of *C. minor* and *C. gratus* (Archibald, 1982): the cusps are conical, increase in size distally, and have longitudinal striations extending from their tips down all sides, to the base of the crown. A tall basal cusp is separated from the medial cusp row by a large notch, and is connected to a smaller cusp by a ridge.

M2: UW 20097 is slightly worn, and the medial cusps as well as the second and third internal cusps were broken postmortem. UCMP 197614 is unworn. The cusp formulae are R:4:4 and R:3:4 (Supplementary Data, Table 8S) for UW 20097 and UCMP 197614, respectively. These compare well with R:3:4 for *Cimexomys gratus* (*C. hausoi* of Archibald, 1982) and 1:3:3 for *Cimexomys judithae* (Montellano et al., 2000). The cusp morphology is nearly identical to the M1s of *C. gratus* (Archibald, 1982) and M1s of *C. minor* in this paper. In the Black Butte Station specimens, the lingual cusps are subcrescentic, and the cusps in the medial row are subcrescentic to crescentic and very closely spaced. The valley separating the lingual and medial cusps shows deep pits and fluting. In occlusal view, the crowns exhibit waisting and the distal edges are fairly rounded (Fig. 7F). The small buccal shelf is much less developed than in *C. judithae* and only slightly less developed than in *C. gratus*. The M2 of *C. minor* has not previously been described but has been assumed to be similar in morphology to if not indistinguishable from M2s of *Mesodma* (see discussion below). Associated specimens of *C. judithae* have M1:M2 length ratios of 0.57 (MOR 302) and 0.66 (MOR 322; Montellano et al., 2000), whereas the M1:M2 length ratio of *C. gratus* is 0.70 (based on average lengths of specimens in Archibald, 1982:table 16). If we use the average length of M1s of *C. minor* described in this paper (2.29 mm; Supplementary Data, Table 8S), the M1:M2 length ratio would be 0.72 with UW 20097 as the M2 and 0.78 with UCMP 197614 as the M2. These estimates and the general morphology reasonably justify tentative referral of UW 20097 and UCMP 197614 to *Cimexomys* cf. *C. minor*.

CIMEXOMYS, sp.
(Fig. 7G; Supplementary Data, Table 8S)

Referred Specimen—UCMP 197622, isolated left M1 from UCMP locality V-84215 (= UW loc. V-79032).

Description and Discussion—UCMP 197622 is moderately worn with a broken mesial edge (Fig. 7G). The cusp formula (5:7:3) and measurements (Supplementary Data, Table 8S) are minimum estimates. The buccal cusps are conical with wear on their tips. The medial cusps are pyramidal and become increasingly subcrescentic distally. The three internal row cusps are small, conical, poorly developed, and poorly separated. The length of the internal row is approximately 50% of the crown length. These features are somewhat inconsistent with descriptions of *Cimexomys minor* by Clemens (1964) and Webb (2001). They are consistent with the description of *C. gratus* by Archibald (1982) and for *C. judithae* by Montellano et al. (2000). In overall crown size, UCMP 197622 (L = 3.34 mm) is much larger than previously described M1 specimens of *C. minor* (L = 2.25–2.61; Archibald, 1982:table 15) and *C. judithae* (L = 2.29–2.39; Montellano et al., 2000:table 1), but falls within the range of the Puercan *C. gratus* (L = 3.13–3.62 mm; Archibald, 1982:table 16). UCMP 197622 also falls within the range of *Mesodma thompsoni* (L = 3.27–3.53 mm; Archibald, 1982); however, the conical exterior cusp row is a primitive characteristic in comparison with the derived subcrescentic cusps seen in *Mesodma.* No upper dentition has been described for *Parikimys carpenteri*, but Wilson et al. (2010) interpreted their lower molars as being more derived than *Cimexomys* and less derived than *Mesodma.* Assuming that *P. carpenteri* falls within a similar size range as *M. thompsoni*, it is possible that UCMP 197622 belongs to this recently described taxon. As discussed in Montellano et al. (2000), *Cimexomys* is a genus with many inconsistencies whose morphology varies greatly across species and within species. Because UCMP 197622 has morphological similarities with *C. minor*, *C. gratus*, and *C. judithae*, we refer it to *Cimexomys*, sp. indet.

?NEOPLAGIAULACIDAE Ameghino, 1890
(Supplementary Data, Table 9S)

Referred Specimens—UCMP 197639 and 197665, both isolated right p4s; UCMP 197612, isolated right m1; UCMP 197618, isolated right M2; and UCMP 197660, left M2, all from UCMP locality V-84215 (= UW loc. V-79032). UW 20139, isolated left p4; UW 15165, 20075, 20090, 20117, all isolated right m1s; UW 20048, isolated left m1; UW 15162, 15194, 20042, 20063, 20065, 20091, isolated left m2s; and UW 15163, 15176, 20043, 20069, 20082, 20102, isolated right m2s, all from UW locality V-79032 (= UCMP loc. V-84215). UW 20136, isolated right m1, from UW locality V-79033.

Comments—All specimens allocated here are morphologically difficult to distinguish between the genera *Mesodma*, *Parikimys*, and *Cimexomys* due to wear, breakage, or other factors (see discussion below). Due to the uncertain phylogenetic placement of *Cimexomys* and the *Paracimexomys* group, we tentatively assign these to ?Neoplagialacidae.

Description and Discussion—p4: UCMP 197639, UCMP 197665, and UW 20139 are p4 distal fragments that fall in the size range of *Cimexomys*, *Mesodma*, and *Parikimys* (Lillegraven, 1969; Archibald, 1982; Wilson et al., 2010). However, because these taxa are mainly distinguished on the basis of p4 arc profile, serration count, and crown length to height ratio, genus-level identifications are not possible.

m1: The cusp formula for six of seven specimens is 6:4, and the remaining m1 (UW 15165) has the cusp formula 7:4 (Supplementary Data, Table 9S). Moderate to severe wear or postmortem damage has obscured the cusp morphology of most specimens (UW 15165, 20048, 20090, 20117, 20136). Although the waisting found midway along the crown length in UW 20117 and 20075 is characteristic of *Parikimys*, we cannot confidently identify these specimens beyond *Cimexomys*, *Mesodma*, or *Parikimys.* Species within these genera overlap in size and are difficult to distinguish on the basis of isolated specimens (Lillegraven, 1969; Archibald, 1982; Webb, 2001; Wilson et al., 2010).

m2: Seven of the 12 specimens have a cusp formula of 4:2, and the other five have a cusp formula of 5:2 (Supplementary Data, Table 9S). The only known m2 of *Parikimys* has a cusp formula of 4:2 (Wilson et al., 2010); whereas most m2s of *Mesodma* have a cusp formula of 3:2 (Archibald, 1982) and m2s of *Cimexomys minor* are unknown. Nearly all of the Black Butte Station m2s have subcrescentic cusps similar to those in m2s of *Parikimys* and *Mesodma* but in contrast to molars of *Cimexomys*. The size range of Black Butte Station specimens (L = 1.33–1.76 mm; Supplementary Data, Table 9S) overlaps the size range of *M. formosa* (L = 1.25–1.60 mm; Archibald, 1982), includes the size of the only described m2 of *P. carpenteri*, and barely overlaps the size range of *M. thompsoni* (L = 1.75–2.15; Archibald, 1982).

M2: UCMP 197618 and 197660 are similar in crown dimensions and cusp morphology to M2s of *Mesodma formosa* and *M. thompsoni.* However, the cusp formulae (2:4:4 and 2:3:4, respectively) are high relative to known species of *Mesodma* (typically 1:3:3; Archibald, 1982). Although *Cimexomys minor* and *Parikimys carpenteri* are not yet known by M2s, molar cusp formulae of *Cimexomys minor* tend to be lower than those of *Mesodma*, whereas the m2 of *P. carpenteri* has a higher cusp formula than m2s of *Mesodma* do (Wilson et al., 2010). However, because of morphological overlap among *Mesodma*, *Cimexomys*, and *Parikimys*, we cannot confidently refer UCMP 197618 and 197660 to one of these genera.

MULTITUBERCULATA Cope, 1884
Gen. et sp. indet.

Referred Specimens—UCMP 197629, 197637, 197646, isolated p4s; UCMP 197649, isolated m2; and UCMP 197643, isolated M1, all from UCMP locality V-84215 (= UW loc. V-79032). UW 15177, 17039 isolated m2s; UW 20061, 25165, 25166, isolated M1s; and UW 15149, 15151, 20059, isolated M2s, all from UW locality V-79032 (= UCMP loc. V-84215).

Remarks—These specimens are fragmentary, extremely worn, or poorly preserved and thus cannot be identified beyond Multituberculata.

HETEROGENEITY IN FAUNAL COMPOSITION AMONG MULTITUBERCULATE ASSEMBLAGES FROM THE WESTERN INTERIOR OF NORTH AMERICA

Understanding heterogeneity in faunal composition among Late Cretaceous and Paleocene biotas is critical to understanding the complexity of K-Pg extinction, survivorship, and recovery dynamics (e.g., Fox, 1968; Jablonski, 1998). What we have learned about the K-Pg event from terrestrial biotas of the northern Great Plains (e.g., Archibald and Bryant, 1990; Johnson, 1992; Pearson et al., 2002; Wilson, 2005, 2009, in press) may not fully apply outside of that area. Spatial heterogeneity could also impact the geographic range over which Lancian and Puercan biochronologic zonations apply (Valentine, 1963; Weil, 1999; Williamson and Weil, 2008; Peppe et al., 2009). Various workers have suggested that northern and southern provinces existed among Late Cretaceous and Paleocene terrestrial biotas of the Western Interior of North America (for plants: Wolfe and Upchurch, 1987; Nichols and Sweet, 1993; for dinosaurs: Lehman, 1997, 2001; Carr and Williamson, 2005; Sampson et al., 2010; for mammals: Anthony and Maas, 1990; Rowe et al., 1992; Weil, 1999; Cifelli, 2000; Cifelli et al., 2004; Davis, 2007; Williamson and Weil, 2008; Wilson et al., 2010). Other workers have argued for greater homogeneity among at least Late Cretaceous terrestrial biotas, indicating that perceived biogeographic differences among northern and southern biotas may be due to weak sampling (Vavrek and Larsson, 2010), temporal differences (Hunter et al., 1997; Sullivan and Lucas, 2006), local paleoenvironmental differences (Hunter et al., 1997), or some combination of those factors and biogeography. The picture may be further complicated by some evidence from dinosaurian (Lehman, 1997, 2001; Carr and Williamson, 2005) and mammalian local faunas (Weil, 1999; Cifelli et al., 2004; Davis, 2007; Williamson and Weil, 2008) that indicate northern and southern provinces might have been the most distinct during the late Campanian Judithian NALMA and weaker to nonexistent during the late Maastrichtian Lancian NALMA. A major issue in resolving these patterns is that fossil sampling, particularly for the Lancian NALMA, is highly skewed toward the northern part of the Western Interior (Wilson et al., 2010:fig. 1), limiting the latitudinal range across which robust quantitative comparisons can be made (but see Weil, 1999; Sampson et al., 2010; Vavrek and Larsson, 2010).

Some recent field work in Lancian-aged deposits of the Cheyenne Basin, northeastern Colorado (Wilson et al., 2010), the Denver Basin, Colorado (Wilson, unpublished), and the San Juan Basin, New Mexico (Williamson and Weil, 2008), has made progress toward improving the representation of the central and southern parts of the Western Interior in the mammalian fossil record. Preliminary findings show that (i) some Lancian mammalian taxa, such as *Mesodma* and *Protolambda*, have far-reaching latitudinal ranges (Wilson et al., 2010); (ii) other newly discovered taxa (e.g., *Parikimys*, *Paressonodon*) are more geographically restricted (Wilson et al., 2010); and (iii) despite some similarity in taxonomic composition, community structure in at least one southern local fauna (Alamo Wash) is distinct from that typical of northern faunas (Williamson and Weil, 2008). Nevertheless, published fossil sample sizes from these local faunas are still too small (<75 identifiable mammalian specimens) for robust quantitative analyses.

The mammalian fossil assemblage from the Black Butte Station (BBS) local fauna is the largest and most diverse yet known from the central or southern part of the Western Interior of North America (Wilson et al., 2010:fig. 1). The 143 multituberculate specimens described here represent eight genera and 11 species (Table 1). Of those taxa, the newly described *Cimolodon peregrinus* is unique to the BBS local fauna, though the possibility remains that it has been misidentified as *C. nitidus* in other collections. *Parikimys carpenteri* and *Paressonodon nelsoni*, which are also members of the BBS local fauna, were first described from slightly farther south in the Cheyenne Basin of northeastern Colorado (Wilson et al., 2010); *P. nelsoni* is now also known by a single specimen from the Hell Creek Formation of Garfield County, Montana (Wilson, in press). *Cimexomys minor* is, in addition to the BBS local fauna, known from the type Lance local fauna (Clemens, 1964) in eastern Wyoming, Hewitt's Foresight One local fauna in northwestern Wyoming, and the Hell Creek Formation in northeastern Montana (Archibald, 1982; Lofgren, 1995; Webb, 2001); it is not recorded in well-sampled but more northerly local faunas from Canada (Lillegraven, 1969; Storer, 1991). Thus, with a few notable exceptions, the BBS multituberculate taxa are typical of local faunas from the northern part of the Western Interior (Cifelli et al., 2004). Williamson and Weil (2008), however, observed that the patterns of relative abundances of taxa in the Alamo Wash local fauna were what made it distinct from the northern local faunas. Two Lancian genera (*Essonodon*, *Glasbius*) that are typical but usually rare in northern local faunas are relatively abundant in the southern Alamo Wash local fauna (San Juan Basin, New Mexico). Hunter and Archibald (2002) also found significant spatial trends in relative abundances in a quantitative analysis of a data set that included local faunas from western Canada to central Wyoming. For example, *Meniscoessus robustus* was abundant among more southerly local faunas and more rare in northern local faunas.

Analyses of Faunal Similarity

Faunal Data—To further investigate the hypothesis that community structure of local faunas differs within the Western Interior of North America, we compiled relative abundance data of multituberculate genera from well-sampled Lancian local faunas (>90 total mammal specimens) from as far north as the Trochu local fauna from the Scollard Formation of Alberta to as far south as the BBS local fauna in southwestern Wyoming. The data are from Hunter and Archibald (2002:table 5) with (i) an update to the Hell Creek Ekalaka data (Zhang unpublished M.S. thesis in Archibald et al., 2011); (ii) replacement of the Hell Creek Garfield data with data from four stratigraphically distinct local faunas from Wilson (2005, 2009, in press); and (iii) addition of the data from the BBS local fauna (this paper) and Hewitt's Foresight One local fauna (Webb, 2001). The addition of the BBS local fauna expands the geographic range southward beyond what was previously possible in Hunter and Archibald (2002). The addition of four stratigraphically distinct local faunas from the Hell Creek Formation of northeastern Montana provides some insight into the temporal influence on the data set. The duration of the Lancian NALMA is not defined, but local faunas included in the data set may vary in age by as much as 2 Ma (Cifelli et al., 2004; Wilson, 2005; Wilson et al., 2010:fig. 1). Instead of species-level data that were used in Hunter and Archibald (2002), we used genus-level data because they are generally more taxonomically robust and avoid uncertainties in specimens that were tentatively identified to species (e.g., *Cimexomys* cf. *C. minor*). The raw abundances are in Table 2. For all analyses, the raw abundances were square-root-transformed and then double-standardized to the maximum abundance of each species (i.e., every taxon has a maximum value of 1.0 in at least one sample) and the total of the sample. These procedures balance the influence of rare and common taxa and large and small samples (Faith et al., 1987; Hammer and Harper, 2006). The double standardization procedure also tends to improve the correspondence of rank ordering among different dissimilarity indices (Oksanen, 2006).

Cluster Analyses—We subjected the transformed and standardized data set to cluster analysis to investigate groupings of local faunas and taxa (Q- and R-mode, respectively). Hierarchical clustering was generated using the UPGMA (unweighted pair group method with arithmetic mean) algorithm and the Bray-Curtis similarity measure. This similarity measure was chosen from among many similarity coefficients available (e.g., Shi, 1993; Legendre and Legendre, 1998), based on its robust performance as a measure of ecological distance in simulation studies that tested 10 similarity measures (Faith et al., 1987) and its common usage in community ecology. The analyses and bootstrapping (1,000 replicates) were performed with PAST version 2.12 (Hammer et al., 2001).

Figure 8A shows the two-way dendrogram produced from the cluster analyses. The results from the Q-mode analysis (Fig. 8A) show that BBS community structure, as represented by relative abundances of multituberculates, is distinct from that of all other local faunas in the analysis (100% bootstrap support). The other local faunas form two asymmetrical clusters. The smaller cluster (26% bootstrap support) contains three local faunas from the middle and upper parts of the Hell Creek Formation of southeastern and northeastern Montana (Ekalaka, Hauso 1, Flat Creek). The larger cluster, which is also weakly supported (17% bootstrap), consists of two subgroups: one made up of two Wyoming local faunas (Hewitt's Foresight One, type Lance), and the other made up of Canadian local faunas (Trochu, Gryde) and local faunas from the lower part of the Hell Creek Formation in northeastern Montana (Tuma, Just Past Celeste's). The pattern of multituberculate faunal similarity shown in the Q-mode cluster analysis appears to have a geographic signal. The BBS local fauna from the central part of the Western Interior is separate from all more northerly local faunas; the other Wyoming local faunas group together as do some of the local faunas from eastern Montana and Canada. The patterning is probably influenced by temporal, paleoenvironmental, and taphonomic factors as well (Hunter et al., 1997; Hunter and Archibald, 2002). For example, among the four local faunas from the Hell Creek Formation in Garfield County, northeastern Montana, the two from the upper third of the formation (Hauso 1, Flat Creek) group together but separately from the two from the lower third of the formation (Tuma, Just Past Celeste's), which form their own pairing. These local faunas are from within 50 km of each other but are

TABLE 2. Number of identified multituberculate specimens from Lancian local faunas of the Western Interior.

	Local fauna									
Genus	Trochu[1]	Gryde[2]	HC Tuma[3]	HC Just Past Celeste's[3]	HC Hauso 1[3]	HC Flat Creek[3]	HC Ekalaka[4]	Hewitt's Foresight One[5]	Type Lance[6]	Black Butte Station[7]
Cimexomys	0	0	0	0	0	0	0	7	7	15
Cimolodon	66	4	2	5	47	30	42	32	450	38
Cimolomys	10	18	1	3	0	6	14	27	89	0
Clemensodon	0	0	0	0	0	0	0	0	3	0
Essonodon	0	0	0	0	7	2	6	0	1	5
Meniscoessus	0	2	0	1	17	6	87	15	186	6
Mesodma	168	473	41	41	103	149	529	490	313	31
Neoplagiaulax	0	0	0	0	1	13	0	2	0	0
Paracimexomys	9	1	0	0	1	26	0	0	0	1
Paressonodon	0	0	0	0	0	0	0	0	0	5
Parikimys	0	0	0	0	0	0	0	0	0	5
Totals	253	498	44	50	176	232	678	573	1049	106

[1]Trochu local fauna, Scollard Fm., Alberta; [2]Gryde local fauna, Frenchman Fm., Saskatchewan; [3]Garfield and McCone counties assorted local faunas, Hell Creek Fm., Montana; [4]Ekalaka local faunas, Hell Creek Fm., Montana; [5]Hewitt's Foresight One local fauna, Lance Fm., Wyoming; [6]Type Lance local fauna, Lance Fm., Wyoming; [7]Black Butte Station local fauna, Lance Fm., Wyoming (this study).

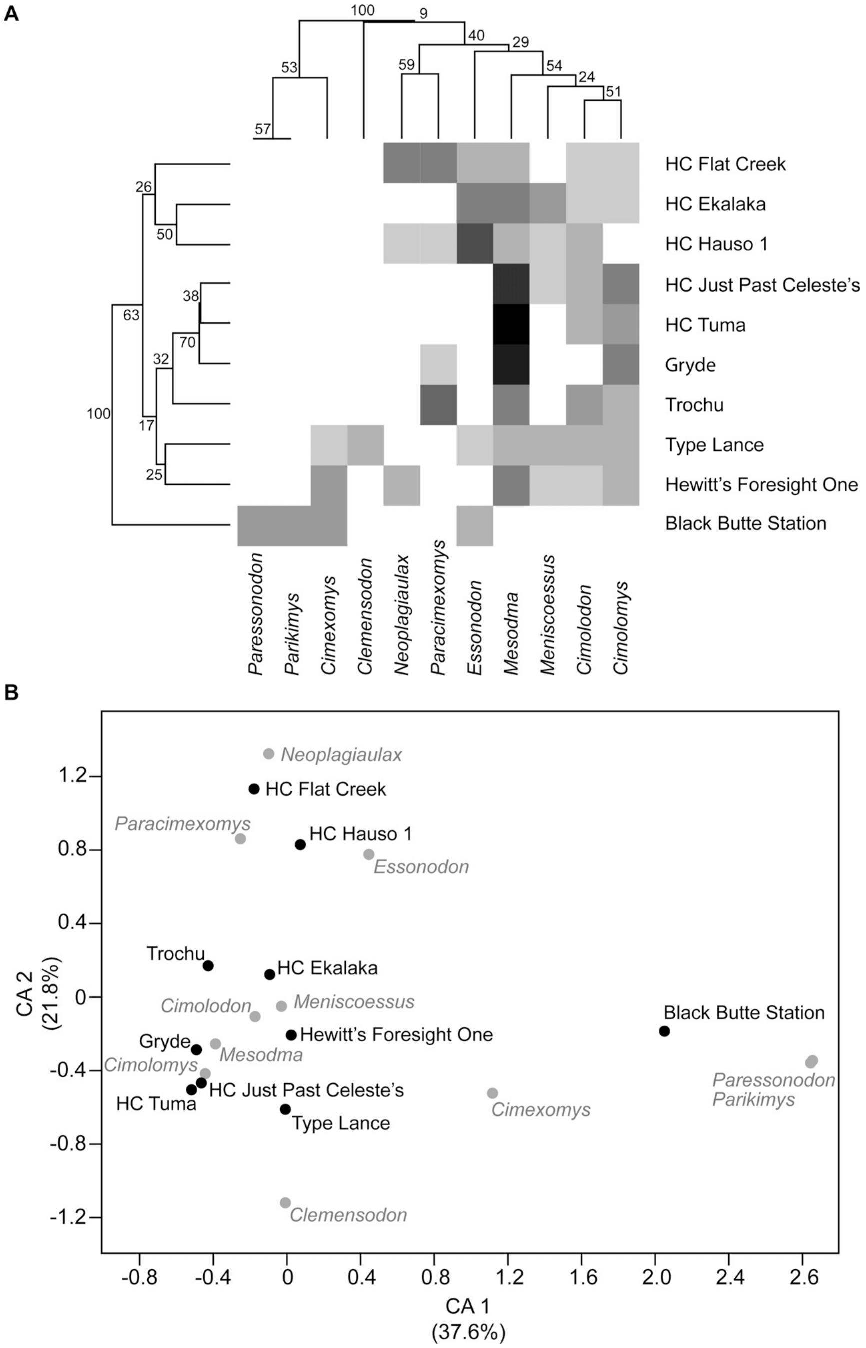

FIGURE 8. **A**, two-way dendrogram produced from Q- and R-mode cluster analyses of well-sampled Lancian local faunas (>90 total mammal specimens) based on square-root-transformed and double-standardized relative abundance data of only the multituberculate genera. Bray-Curtis similarity measure was used to generate the distance matrix and UPGMA for the agglomerative algorithm. Shaded cells indicate the relative abundance of each taxon in each local fauna, with the gradient from white to black increasing at 20% intervals. Bootstrap percentages are presented at each node based on 1000 replicates. **B**, a plot of the first two axes generated from a correspondence analysis of the same data set. Gray dots and text represent scores for each taxon; black dots and text represent scores for each local fauna. The first two axes capture a total of 59.4% of the variance. **HC Flat Creek**, Flat Creek local fauna, Hell Creek Fm., Garfield County, Montana (Wilson, 2005); **HC Ekalaka**, Ekalaka local fauna, Hell Creek Fm., Montana (Zhang, unpublished M.S. thesis, in Archibald et al., 2011); **HC Hauso 1**, Hauso 1 local fauna, Hell Creek Fm., Garfield County, Montana (Wilson, 2005); **HC Just Past Celeste's**, Just Past Celeste's local fauna, Hell Creek Fm., Garfield County, Montana (Wilson, 2005); **HC Tuma**, Tuma local fauna, Hell Creek Fm., Garfield County, Montana (Wilson, 2005); **Gryde**, Gryde local fauna, Frenchman Fm., Saskatchewan (data from Hunter and Archibald, 2002, and references therein); **Trochu**, Trochu local fauna, Scollard Fm., Alberta (data from Hunter and Archibald, 2002, and references therein); **Type Lance**, Type Lance local fauna, Lance Fm., eastern Wyoming (data from Hunter and Archibald, 2002, and references therein); **Hewitt's Foresight One**, Hewitt's Foresight One local fauna, Lance Fm., northwestern Wyoming (data from Webb, 2001); **Black Butte Station**, Black Butte Station local fauna, Lance Fm., southwestern Wyoming (this study). See Figure 1 for geographic distribution of local faunas.

separated in time by at least 1 Ma (Wilson, 2005, 2009, in press). The Hell Creek Ekalaka local fauna, which groups with Hauso 1 and Flat Creek, is from the middle third of the Hell Creek Formation in nearby southeastern Montana (Hunter and Archibald, 2002; Archibald et al., 2011). Detailed temporal or stratigraphic data for most of the other local faunas are less certain (but see Wilson et al., 2010:fig. 1B). The paleoenvironmental and taphonomic data for each of the localities are also limited, but should be a goal of future research.

The dendrogram (Fig. 8A) resulting from the R-mode analysis shows taxonomic associations that are present in the faunal similarity data. *Cimexomys*, *Paressonodon*, and *Parikimys* group together (53% bootstrap support) and separately from all other taxa. They co-occur in only the BBS local fauna. *Cimexomys* also occurs separately in the other Wyoming local faunas and with *Paressonodon* in the Hell Creek Formation of northeastern Montana (Wilson, in press) but not in the well-sampled local faunas included in our data set. *Parikimys* and *Paressonodon* are also found together in the small fossil assemblage from the Lancian-age Ingrid's Jaw locality in the Cheyenne Basin of northeastern Colorado (Wilson et al., 2010). In the large cluster formed by all other multituberculate taxa, *Clemensodon*, which has only been recorded in the type Lance local fauna (Krause, 1992), forms the most basal branch. The remaining taxa form two subgroups. In one subgroup, *Paracimexomys* and *Neoplagiaulax*, which co-occur in the Flat Creek and Hauso 1 local faunas, are paired together (59% bootstrap). The other subgroup is formed by taxa that occur in nearly all of the local faunas. *Essonodon* is the most notable exception; it has a stratigraphic range that is restricted to the middle and upper thirds of the Hell Creek Formation of northeastern Montana (i.e., late C30n–C29r; Wilson, 2005). Thus, its shared absence in the Tuma and Just Past Celeste's local faunas from the lower part of the Hell Creek Formation of northeastern Montana and the Gryde local fauna from the Frenchman Formation of southern Saskatchewan might indicate a similarity in age. In turn, its presence in the BBS local fauna (and the Alamo Wash local fauna of New Mexico; Williamson and Weil, 2008) might indicate that the BBS local fauna is similar in age to the local faunas from the middle and upper Hell Creek Formation (Hauso 1, Flat Creek). Alternatively, *Essonodon* may have been present earlier in lower latitude faunas, if it immigrated from lower latitudes to higher latitudes as temperatures rose in the last ~500 ka of the Cretaceous (Wilf et al., 2003; Wilson, 2005).

Ordination Methods—Hierarchical clustering methods force groupings of samples or variables (Q- and R-mode, respectively) in data sets that might be better represented as gradients (e.g., latitudinal gradient) rather than discrete groupings. For example, Hunter and Archibald (2002) used correspondence analysis (CA) to analyze spatial patterning in mammalian faunal data from the northern part of the Western Interior. We applied four ordination methods to the multituberculate data set: CA, detrended correspondence analysis (DCA), principal coordinates analysis (PCO), and non-metric multidimensional scaling (NMDS). NMDS and DCA are perhaps the two most popular ordination methods currently used in community analyses. They avoid the arch effect that can plague PCO (also called metric multidimensional scaling) as well as CA (Hammer and Harper, 2006). NMDS ordinates the data in a fashion similar to that done by PCO except that it transforms absolute distances into rank distances (Legendre and Legendre, 1998). This approach, however, is highly sensitive to the similarity index and the number of dimensions selected for ordination. Moreover, NMDS uses an iterative process rather than an algorithm to arrive at the ordination solution, leaving open the possibility that it represents the best local solution but not the best global solution (Legendre and Legendre, 1998). DCA alleviates some flaws of CA through a detrending and rescaling manipulation that is viewed by some as ad hoc and without theoretical justification (Wartenberg et al., 1987). Conversely, it is better suited than NMDS for testing gradient hypotheses (Peet et al., 1988), such as latitudinal differentiation of mammalian local faunas. We performed the analyses with PAST version 2.12 (Hammer et al., 2001), using the Bray-Curtis similarity index for PCO and NMDS. CA and DCA use chi-square distance. For DCA, we varied the number of segments from 5 to 40, but found no change in Axis 1 or the relative position of local faunas along Axis 2.

Despite the differences in the methods outlined above, ordinations of the multituberculate local faunas on the first two axes were nearly identical among methods. The plots differ in the degree of separation among data points but not in the relative position or composition of major groupings. We only present the results from the CA (Fig. 8B). The first two axes of the CA explain 37.6% and 21.8% of variance, respectively, for a total of 59.4% of the variance. The ordination of local faunas and taxa on the first two axes is broadly consistent with the Q-mode and R-mode cluster analyses. The BBS local fauna, which has a very high score on Axis 1 (2.06), is separated from all other local faunas, which have low scores on Axis 1 (−0.51–0.08). *Parikimys*, *Paressonodon*, and to some degree *Cimexomys* also have high scores on Axis 1. Axis 2 separates local faunas of the upper part of the Hell Creek Formation in northeastern Montana (Hauso 1, Flat Creek) from all other local faunas. *Neoplagiaulax*, *Paracimexomys*, and *Essonodon* also ordinate high on Axis 2, whereas *Clemensodon* is very low on Axis 2.

Testing for Spatial Correlation—To test whether these taxonomic composition and relative abundance patterns correlate with spatial gradients, we used a modified Mantel test of matrix correspondence (Smouse et al., 1986) in the Ecodist package version 1.2.7 (Goslee and Urban, 2007) for the statistical program R version 2.10.1 (R Development Core Team, 2009). Specifically, we measured the correspondence of the pairwise faunal distance matrix of the local faunas (derived from the Bray-Curtis similarity measure) and three different pairwise geographic distance matrices of the local faunas. The geographic data for each local fauna were derived from the present-day latitude and longitude of each site (e.g., Hunter and Archibald, 2002:table 7). In the first comparison, geographic distance was measured as the pairwise Euclidean distance between local faunas. This comparison tests for the influence of spatial autocorrelation, which may be viewed as the null hypothesis that the observed faunal differences are simply the product of geographic distance between local faunas rather than a specific directional gradient (e.g., longitude, latitude). The Mantel coefficient for this comparison was positive but fairly low (0.204) and not statistically significant on a two-tailed test ($P = 0.369$). The second comparison, which used geographic distances as measured by pairwise longitudinal differences between local faunas, tests whether the differences in faunal composition among the local faunas correlate with longitude and the factors relating to longitude (e.g., proximity to the Western Interior Seaway). The Mantel coefficient was negative and very low (−0.098) and not statistically significant ($P = 0.632$). The third comparison, which used geographic distance as measured by latitudinal differences between local faunas, tests whether the differences in faunal composition among the local faunas correlate with latitude and the factors relating to latitude (e.g., climate). The Mantel coefficient was positive and relatively high (0.355) but not quite statistically significant at the alpha level of 0.05 ($P = 0.073$). Together, these results indicate that the faunal differences are not simply the product of geographic distance between local faunas and do not seem strongly related to proximity to the Western Interior Seaway. Although the faunal differences do not significantly correlate with latitude, this relationship showed the best fit to the present data set. Hunter and Archibald (2002) found that in their data set, which was geographically more restricted but taxonomically more inclusive (i.e., therians and multituberculates), the latitudinal signal was more likely an artifact of geographic distance. Future tests of these hypotheses may be strengthened by inclusion of additional taxa (e.g., therians) and by inclusion of additional local faunas that expand the latitudinal and longitudinal coverage, particularly as sampling of local faunas from the central and southern parts of the Western Interior improves and other possible contributing factors (e.g., paleoenvironment, age, taphonomy) are better understood for each local fauna.

REFUGIA AS A SOURCE FOR EARLY PALEOCENE IMMIGRANTS

In the earliest Paleocene (Pu1 of the Puercan NALMA), a number of mammalian taxa make an abrupt first appearance in the Western Interior of North America (Clemens, 2010); they include some archaic ungulates, eucosmodontid multituberculates, and taeniolabidid multituberculates (Lofgren et al., 2004). For the most part, they lack credible ancestors in local or even regional latest Cretaceous (Lancian) faunas (Weil and Clemens, 1998). The source area(s) for these immigrants or 'aliens' (Weil and Clemens, 1998) remains unknown, but hypotheses point to possibilities in Asia (Lillegraven, 1969; Kielan-Jaworowska and Sloan, 1979; Nessov et al., 1998), Baja California (Weil and Clemens, 1998), and unsampled upland or inland refugia in the Western Interior (e.g., Fox, 1968; Weil, 1999; Weil and Krause, 2008; Clemens, 2010). Discriminating among these hypotheses and gaining a better understanding of K-Pg recovery dynamics is dependent upon better sampling of latest Cretaceous local faunas in these potential source areas. This was one of our primary motivations for studying the BBS mammalian fossil assemblage.

In addition to being farther south than most well-sampled local faunas from the Western Interior, the BBS local fauna was located in a distinct paleoenvironment farther inland and possibly upland from the coastal lowlands along the Western Interior Seaway. As such, it offers a chance to test the refugia hypothesis. In a preliminary summary of the mammalian fauna from BBS, Breithaupt (1982) listed, among typical Lancian taxa, the possible occurrence of *Protungulatum* sp., an archaic ungulate that at that time was otherwise only confirmed from Puercan local faunas (but see Archibald et al., 2011). The occurrence of *Protungulatum* in the Lancian BBS local fauna remains unconfirmed, and the lack of 'aliens' (e.g., eucosmodontids, taeniolabidids) among the multituberculates from the BBS local fauna does not support the hypothesis of this area as a refugium. Nevertheless, the BBS local fauna has not been fully studied and it represents one sample from a broader, underrepresented area. Perhaps within other inland, upland, and/or paleoenvironmentally distinct local faunas, we might identify a source of Puercan 'aliens.'

SUMMARY

The multituberculate assemblage from Black Butte Station (BBS) area presently provides our best view of a mammalian local fauna from the poorly sampled central part of the Western Interior of North America. The 143 multituberculate mammal specimens represent eight genera and 11 species, including a new larger-bodied species *Cimolodon peregrinus* and the second published occurrences of *Paressonodon nelsoni* and *Parikimys carpenteri.* Among the multituberculate specimens described, approximately 36% are *Cimolodon*, 29% are *Mesodma*, 14% are *Cimexomys*, and the remainder is distributed across five other genera (Table 1). The high relative abundance of *Cimexomys* in the BBS local fauna is unusual among Lancian local faunas. *Essonodon* also has a fairly high relative abundance (4.72%) that, among more northerly local faunas, is only approached in the Hauso 1 local fauna (3.98%) of northeastern Montana. Williamson and Weil (2008), however, reported an elevated relative abundance of *Essonodon* in the more southerly Alamo Wash local fauna from the San Juan Basin of New Mexico. The presence of *Essonodon* in the BBS local fauna also provides support for a Lancian age (Cifelli et al., 2004; Wilson, 2005; Williamson and Weil, 2008). Notably absent from the BBS local fauna is *Cimolomys*; this may represent true absence, sampling deficiency, taphonomic bias, or misidentification. Quantitative comparisons (cluster and ordination analyses) of multituberculate community structure among well-sampled mammalian local faunas (>90 total mammalian specimens) from the Western Interior of North America demonstrate that the BBS local fauna is distinct from all other local faunas and that the patterns of variation in the data most strongly correlate with latitude (though not significantly so). Various other factors (e.g., age, paleoenvironment, geographic distance, taphonomy) may also correlate with this pattern. Local faunas from the northern part of the Western Interior of North America tend to be dominated by the genus *Mesodma*, whereas at lower latitudes, *Mesodma* is common but less so as *Cimolodon* and *Meniscoessus* become more prevalent; *Paressonodon*, *Parikimys*, and *Cimexomys* also appear to be characteristic among lower latitude faunas.

Although upland and inland refugia have been proposed as possible sources for 'alien' taxa that abruptly appear in the Western Interior following the K-Pg boundary, the multituberculates of the BBS local fauna provide no support for this hypothesis. Nevertheless, it is noteworthy that expanding the sampled paleoenvironment beyond the coastal lowlands along the Western Interior Seaway has increased the sampled biodiversity. In a description of material from the 'Edmontonian' St. Mary River local fauna in Montana, which is characterized as an upland river system, Hunter et al. (2010) described two new taxa and here from an inland setting we described one new taxon. These studies thus argue for the need to continue field efforts to collect from undersampled paleoenvironments and regions to better understand the biogeographic diversity present during this critical interval in order to explore their implications for K-Pg extinction and recovery patterns and regional biochronology.

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